ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE NEW YORK ZOOLOGICAL SOCIETY

VOLUME 54 • ISSUE 2 • SUMMER, 1969

Phonograph Record Inside Back Cover

PUBLISHED BY THE SOCIETY
The ZOOLOGICAL PARK, *New York*

Contents

Manuscripts must conform with *Style Manual for Biological Journals* (American Institute of Biological Sciences). All material must be typewritten, double-spaced. Erasable bond paper or mimeograph bond paper should not be used. Please submit an original and one copy of the manuscript.

ZOOLOGICA is published quarterly by the New York Zoological Society at the New York Zoological Park, Bronx Park, Bronx, N. Y. 10460, and manuscripts, subscriptions, orders for back issues and changes of address should be sent to that address. Subscription rates: $6.00 per year; single numbers, $1.50, unless otherwise stated in the Society's catalog of publications. Second-class postage paid at Bronx, N. Y.

Published November 17, 1969

4

Some Mexican and Central American Land Snails of the Family Cyclophoridae

Fred G. Thompson[1]

(Plates I-VII; Text-figures 1-14)

The systematics of some Middle American cyclophorid snails is revised based on studies of the soft anatomy. Two subfamilies are recognized (Aperostominae and Neocyclotinae) as occurring in Mexico and Central America, not including the Diplommatinid genus *Adelopoma*. The subfamilies are separated by characteristics of the male and female reproductive systems. Genera placed in the Aperostominae include *Aperostoma, Megalomastoma, Farcimen,* and *Tomocyclus*. Genera placed in the Neocyclotinae include *Dicrista* new genus (type species—*D. liobasis* n. sp.), *Xenocyclus* new genus (type species—*X patulus* n. sp.), *Amphicyclotus,* and *Neocyclotus*. The following new species and subspecies are also described: *Dicrista flavescens* n. sp., *D. indentata* n. sp., *D. rugosa* n. sp., *Amphicyclotus texturatus spiralis* n. sp., *A. paulsonorum* n. sp., *Neocyclotus simplicostus* n. sp., *N. capscelius* n. sp., *N.* (*Incidostoma*) *impressus* n. sp. The following nomenclatorial changes are made: *Mexcyclotus petersi petersi* Solem change to *Dicrista petersi* (Solem); *M. p. damianensis* Solem changed to *D. damianensis* (Solem); *Cyclotus cooperi* Tryon changed to *D. cooperi* (Tryon). *Cyclostoma lutescens* Pfeiffer is considered a nomina dubia. The generic name *Mexcyclotus* based on *lutescens* as genotype become unavailable for use among Mexican taxa.

THE purpose of this study is to present new information bearing on the systematics and distributions of some Mexican and Central American cyclophorid snails based on material collected during recent years. The material includes numerous specimens preserved for anatomical investigations, and alters previous systematic concepts. The study is not comprehensive, and includes only critical synonymies for particular species and genera. For a complete review of the taxa within this region the reader is referred to papers by Bartsch and Morrison (1942), Morrison (1955), and Solem (1956).

Introduction

The Cyclophoridae are typical of many groups of neotropical land snails. Although many species are known, more await to be discovered. Most of those that are known are represented by only a few specimens each. Distribution data are sparse or absent for most species. Large geographic areas from which material may be expected remain unexplored for mollusks. Very little is known about individual or geographic variation, and much less is known about the anatomies of the various species.

The classification of the cyclophorid mollusks is as confused as that of any other comparable division of land mollusks. There is no general agreement whether the cyclophorids comprise a single very large family, or whether several distinct families are involved. Recent authors tend to recognize the group as a superfamily with several families, but no one has demonstated the presence of characters that consistently separate and characterize the families. All of the genera discussed in this paper are placed in a single family and assigned to two subfamilies. This does not imply that I favor the recognition of a single large family, the Cyclophoridae, but only that I am hesitant to recognize additional families until more is learned about the soft anatomy of the various divisions. Families or subfamilies in this group currently are based, in part, on the geographic distributions of these categories, and this leaves much

[1] Florida State Museum, University of Florida, Gainesville, Florida 32601.

to be desired in explaining their origins, evolution, and relationships.

Early systems of classification divided the helicoid cyclophorids into two subfamilies. Those with a calcified operculum were placed in the Cyclotinae, and those with a chitinous operculum were placed in the Cyclophorinae. The cylindroid genera were placed in several different subfamilies on even lesser basis. This system was modified by Kobelt (1902) and Thiele (1929) who used geographic distribution as an important factor. All of the neotropical genera were placed in a single subfamily with the exception of *Adelopoma,* which belongs in the subfamily Diplommatininae. Bartsch (1942) recognized three subfamilies endemic to the American tropics, but made no attempt to differentiate them from Old World groups. These subfamilies were based exclusively on shell and opercular characters. The helicoid genera were placed in the Aperostominae with a calcified operculum, and the Amphicyclotinae with a chitinous operculum. The cylindroid genera were placed in the Megalomastominae.

Tielecke (1940) divided the cyclophorid mollusks into five families, based primarily on the anatomy of the reproductive systems. His contribution is outstanding in that it was the first and only comprehensive attempt to study the soft anatomy of the cyclophorid mollusks. The neotropical genera were placed in a single family, the Poteriidae, characterized by possessing a common duct for the copulatory bursa, oviduct, and the seminal receptacle, and by having the verge in males located on the center of the nape or behind the right tentacle.

Recently Morrison (1955) studied the external male reproductive structures of the neotropical members and placed them in two families, the Amphicyclotidae and the Neocyclotidae. The Amphicyclotidae was characterized by having a seminal duct enclosed within the verge. The Neocyclotidae was characterized by having an open seminal groove extending to the tip of the verge, and included two subfamilies, the helicoid Neocyclotinae (= Aperostominae and Poteriidae of other authors) and the cylindroid Neopupinae (= Megalomastominae). He related the Neocyclotidae to the Cyclophoridae but derived the Amphicyclotidae from the marine family Lacunidae. Solem (1957) demonstrated that *Amphicyclotus* possesses a verge that places it in the Neocyclotidae, and indicated the nomenclatural changes that were necessary if the West Indian "amphicyclotids" were recognized as a separate subfamily. Thompson (1967) showed that this West Indian group is related to the neocyclotids by the structure of the female reproductive system, but differed conspicuously in the tubular structure of the verge, and recognized the group as the subfamily Crocidopominae.

Recent field work in Mexico and Central America has produced much new and interesting material of the Cyclophoridae. This material represents several new taxa and adds distributional data to some species that previously were known from indefinite localities. Even more important, most of the species collected are represented by soft parts, which provide new evidences on the phylogeny of the group in Middle America. New descriptions of four poorly known species are also included.

Acknowledgment

Many people have assisted me in this study, to all of whom I am grateful. For assistance in field work in Mexico and Central America I wish to thank Dennis R. Paulson and his wife Mary Lynn, Washington State University; F. Wayne King, New York Zoological Society; Roy McDiarmid, Norman Scott, and Jay Savage, University of Southern California; Andrew Starrett, Los Angeles County Museum of Natural History; Colin Little, University of Bristol; S. David Webb, Florida State Museum, University of Florida (UF). Albert Schwartz and Richard Thomas, Miami, Florida, have provided me with much valuable West Indian material. I wish to thank the following people for the loan of specimens in their charges. Tucker Abbott, Academy of Natural Sciences, Philadelphia (ANSP); Henry van der Schalie, Museum of Zoology, University of Michigan (UMMZ); Harold A. Rehder, United States National Museum (USNM). Photographs of shells used in this paper were taken by Ernest M. Collins, Jr., staff photographer of the Florida Division of Plant Industries. Field work in Mexico and Central America was supported by the National Institutes of Health Research Grant GM 12300.

Family Cyclophoridae

The material that I have studied alters previous classifications of the neotropical cyclophorids. All apparently lack a copulatory bursa such as occurs in *Cyclophorus* (Tielecke, 1940: 321-327). I found no structure that appears homologous to that organ of the Old World cyclophorids. The absence of this organ indicates a degree of unity among the American genera that may justify recognition of them as a single family, the Neocyclotidae. However, the anatomical diversity of these genera overshadows the common relationships suggested by the absence of the bursa. The Megalomastominae differs from all other cyclophorid groups by

having a long vaginal slit extending nearly the length of the uterus. The subfamily is also peculiar among New World groups in having a multipapillaform seminal receptacle and a verge located on the side of the head behind the right tentacle. These last two characters suggest a relationship with the Asiatic Pupininae (-idae). Characters of the shell also suggest this relationship, but the Asiatic pupinids differ by having a well developed copulatory bursa. Until more is learned about the anatomy or the various Asiatic pupinid genera, the relationship between the Pupininae and the Megalomastominae will remain in question.

The Neocyclotinae and the Crocidopominae are more alike to each other than to any other comparable group of cyclophorids by having a verge that is located on the center of the nape. The Neocyclotinae has a stout verge that bears an open seminal groove extending from the end of the prostate to the tip of the penis. The Crocidopominae has a long slender verge that possesses a tubular seminal duct. Apparently the Crocidopominae evolved from the Neocyclotinae. The emphasis placed on the distinction between these two subfamilies may be questionable, but their relationships and their differences are clear in contrast to most other cyclophorid subfamilies.

Subfamily Megalomastominae Kobelt and Mollendorff

The external male reproductive structures of the following species have been described:

Aperostoma m. mexicana (Menke) (Tielecke, 1940: 339)
Aperostoma walkeri Baker (Morrison, 1955: 152)
Tomocyclus simulacrum (Morelet) (Bartsch and Morrison, 1942: 142)
Farcimen vinalense scopulorum T. and B. (Torre and Bartsch, 1942: 34)
Farcimen superbum itinerium T. and B. (Morrison, 1955: 152)
Farcimen (*Neopupina*) *croteum* (Gmelin) (Bartsch, 1942: 44)
Megalomastoma pepiti Bartsch (Bartsch, 1942: 48)

In addition I have examined both sexes of the following species:

Aperostoma mexicana salleana (Martens)
Aperostoma palmeri (Bartsch and Morrison)
Farcimen (*Neopupina*) *croteum* (Gmelin)

This subfamily is characterized by having the penis located on the side of the head behind the right tentacle. The penis is broad and flattened basally, and becomes cylindrical and attenuate distally. An open seminal groove extends from the end of the prostate and along the side of the nape to the penis where it passes along the outer and lower margin to the tip. The prostate has a corresponding slit along its columellar margin. The slit opens into the prostatic lumen and extends from the seminal duct to the anterior end of the prostate where it continues with the seminal groove on the nape.

The female has an open vaginal slit that extends almost the length of the uterus and is continuous with the uterine lumen. The uterus has a single continuous lumen and is multilobate along its outer and distal margins. The copulatory bursa is rudimentary or absent. The seminal receptacle consists of a series of digitiform or grape-like glandular lobes that discharge into a common chamber. The albumen gland is formed by a simple loop in the oviduct and is attached at its base by connective tissue to the side of the bursa. The albumen gland enters into the chamber of the seminal receptacle, which in turn opens into the distal end of the vaginal slit. Both the albumen gland and the seminal receptacle are imbedded in muscle and connective tissue and appressed to the side of the uterus.

In addition the subfamily has an unusually enlarged hypobranchial gland, that occupies a major portion of the surface of the pseudolung (Text-fig. 1).

The megalomastomids have in common a multispiral, cornified operculum in which the outer edges of the whorls overlap the succeeding whorls and project obliquelly outward as thin chitinous lamella. The innermost whorls may be thickened but do not have calcareous deposits. Although these opercular characteristics do not distinguish this group, they show a degree of uniformity among the member genera.

This subfamily consists of a homogeneous group of genera that is confined to eastern Mexico, Guatemala, and the Antilles. Aside from the helicoid genus *Aperostoma* all of the species are cylindroid in shape. This divergence in shape is more apparent than significant, for other features of the shell, such as the siphonal notch and the reflected peristome, indicate a close affinity between *Aperostoma* and *Tomocyclus*, which have allopatric but contigous ranges in eastern Mexico and Guatemala.

Tomocyclus

This genus has recently been reviewed (Thomson, 1963). No additional material has been examined.

Aperostoma mexicanum salleanum (Martens)

Cyclophorus salleanum von Martens, 1865; Malak. Blätt., 12:151. — Strebel, 1873; Beit. Mex. L. — Susswasser Couchy., I: 9; pl. 1,

fig. 2; pl. 1A, figs. 2-2a. – Martens, 1890; Biol. Cent. Amer.: 7-8. (Type locality: Córdoba, Veracruz).

Cyrtotoma mexicanum salleanum (Martens), H. B. Baker, 1922; Occ. Pap. Mus. Zool. Univ. Mich., (106):42-43; pl. 16, figs. 8-12.

Aperostoma mexicanum salleanum (Martens), H. B. Baker, 1928; Occ. Pap. Mus. Zool. Univ. Mich., (193):51.

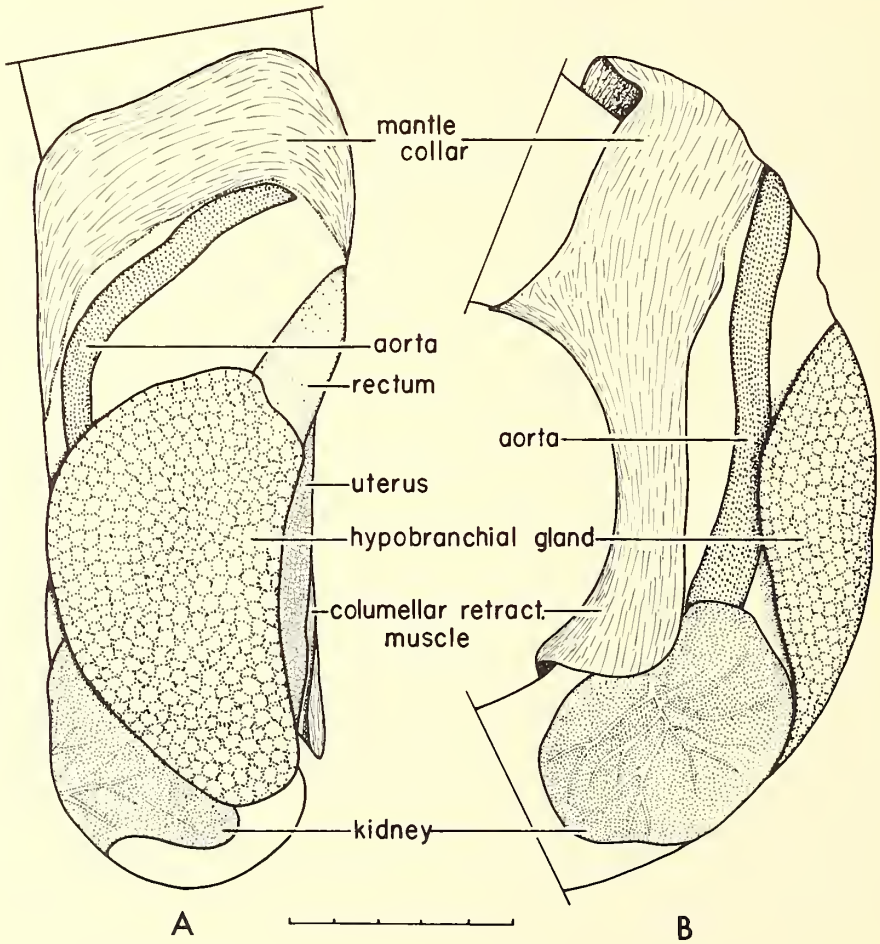
Cyrtotoma salleanum (Martens), Bartsch and Morrison, 1942; Bull. U.S. Nat. Mus., 181: 170-171; pl. 22, figs. 19-21.

Aperostoma m. mexicanum (Menke), Solem, 1956; Proc. Acad. Nat. Sci. Phila., 108:48-50 (*in part*).

Veracruz: 2.9 mi. E. Córdoba, 2500′ (UF 20211. 2); 1.9 mi. S.W., 0.8 mi. N. Fortin, 2900′ (UF 20212 . 1♂); 4.3 mi. E. Córdoba, 2300′ (UF. 1♀). Anatomical material examined from the last two localities.

Male. The penis is located on the side of head behind the right tentacle. The base of the penis is bulbous; the distal end is about twice the length of the base and is slender and flagellate. An open seminal groove extends from the prostate and along the side of the nape to the tip of the penis.

Female. (Text-fig. 2, C) The single female examined illustrates the general features of the reproductive system, although the uterus does not appear to be completely mature. The vaginal slit extends the length of the uterus and is continuous with the uterine chamber. The uterine chamber is uninterrupted through its length. The outer margin of the uterus is convoluted into



Text-fig. 1. *Aperostoma palmeri* (Bartsch and Morrison). Dorsal and lateral view of the pseudolung and associated organs showing the relatively large hypobranchial gland. Scale equals 5 mm.

many small lobes that decrease in size distally. The distal end of the uterus is very thin and spatulate, with weakly indicated lobation. The seminal receptacle consists of about four digitiform glandular lobes that discharge into the oviduct. The albumen gland consists of a simple convoluted loop in the oviduct. The loop is attached to the base of the seminal receptacle by fine fibers of connective tissue.

Aperostoma palmeri (Bartsch and Morrison)

Cyrtotoma palmeri Bartsch and Morrison, 1942, Bull. U.S. Nat. Mus., 181:172-173; pl. 22, figs. 1-3. (Type locality: Gomez Farías, Tamaulipas).

Aperostoma mexicanum palmeri (Bartsch and Morrison), Solem, 1956; Proc. Acad. Nat. Sci. Phila., 108:50-51; pl. 5, figs. 1-4, pl. 6, figs. 1-5.

San Luis Potosi: 11.4 mi. E. Xilitla, 1100′ (UF 20209. 31), (UF 20208. 11): 7.5 mi. E. Xilitla (UF 20210 . 1). One female and one male examined from first locality.

The material before me does not indicate intergradation with *A. mexicana* as Solem (1956: 51) reported for material from the same region. *A. palmeri* is readily distinguished from *A. mexicana* by its deep parietal notch that is open to the dorsal surface of the whorl as a siphonal notch, and by its thickened, weakly flaring peristome. The parietal notch is partially obscured by a wing-like extension of the upper lip which leaves a narrow slit connecting the notch with the margin. *A. mexicana* has a more broadly flaring peristome, and the parietal notch consists of a simple U-shaped indentation that lies along the parietal wall of the aperture, but does not open through the dorsal wall of the whorl as in a siphonal notch.

The nature of the anatomical material is not satisfactory for detailed studies, but does show the gross morphological features of the reproductive systems.

Male. Reproductive system typical for genus. The penis is located on the side of the head behind the right tentacle. The seminal groove extends from the prostate and along the side of the nape to the tip of the penis. The groove is uninterrupted along its course. The prostate lies along the right margin of the pseudolung, and appears to have an open seminal channel that is continuous with the prostatic chamber and extends from the spermatoduct to the anterior end of the prostate. The channel lies along the right margin of the pseudolung, and terminates over the seminal groove on the nape.

Female. The reproductive system is similar to that described for *A. mexicana salleana*, except that the uterus is more developed, and has the same general appearance as does *Farcimen croteum*.

Farcimen (Neopupina) croteum (Gmelin)

Puerto Rico: 2.5 mi. S.W. Yabucoa, 800′ alt. (3 females and 1 male); 1 km. S. Pueblito de Ponce (4 females, 1 male).

Male. The verge is located on the right side of the head behind the tentacle. It has an open seminal groove that is continuous from the prostate.

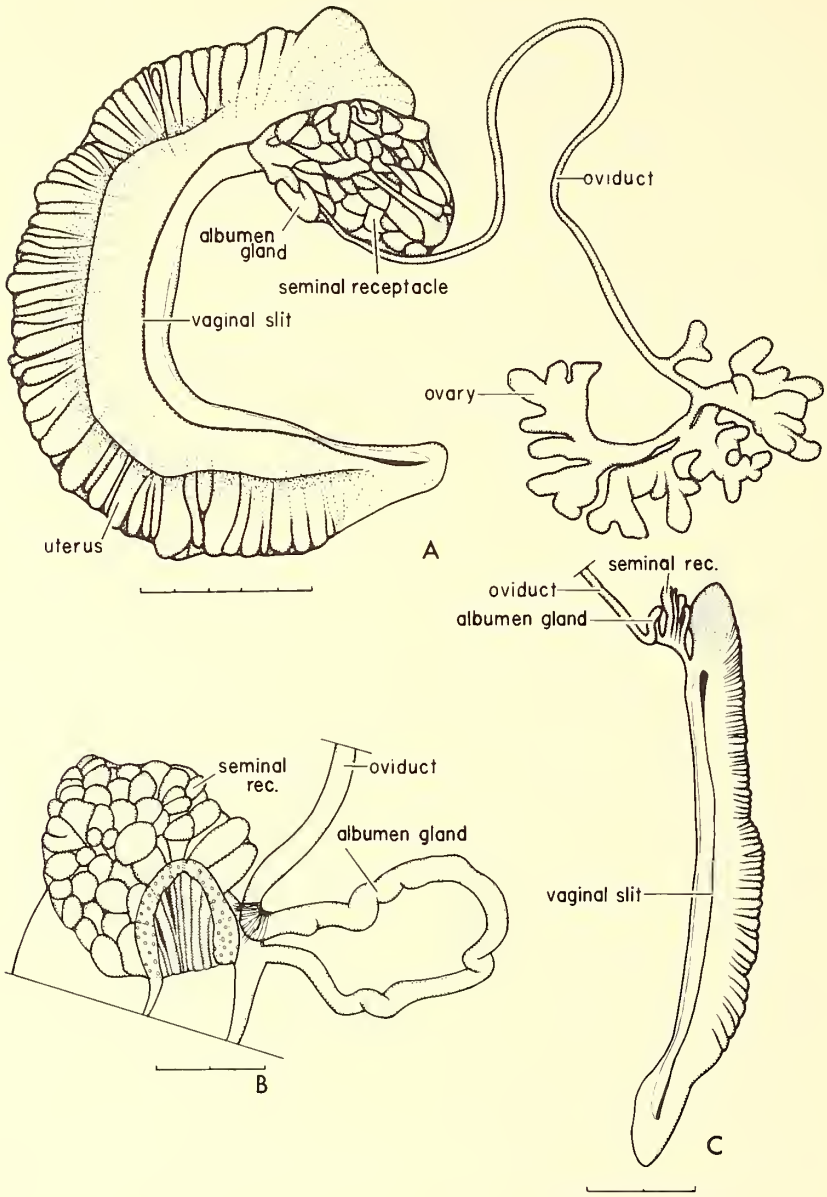
Female. The uterus (Text-fig. 2, A-B) is large, robust, and glandular with numerous large folds along its intestinal margin. The distal end is conspicuously flattened and palmate. The vagina consists of a continuous slit that extends the length of the uterus, and has a very thin membranous fold that overlaps the outer wall of the uterus. The vaginal slit is continuous with the uterine cavity, which continues distally into the seminal receptacle. The receptacle consists of a large mass of closely attached glandular lobes that discharge individually or in small groups into a chamber. The lumen of the receptacle is lined with numerous small folds that ramify into the individual glandular lobes. The albumen gland consists of a long sigmoid loop in the oviduct that is closely attached by connective tissue to the side of the seminal receptacle in such a way that it is not distinguishable from the receptacle lobes upon superficial examination. The ovary consists of five glands. The first gland is a small, single digitiform structure. Subsequent glands are multilobate.

The mantle is similar to that of *Aperostoma* in that the hypobranchial gland is thick and padlike, but is confined to the left side of the pseudolung, is smaller, and is kidney-shaped.

Subfamily Neocyclotinae Kobelt and Mollendorff, 1898

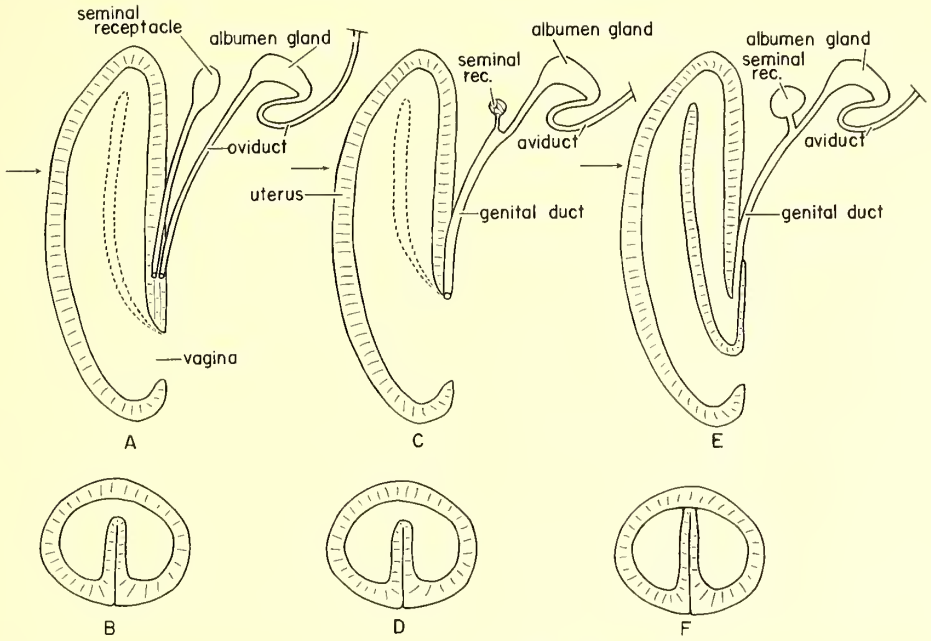
This subfamily includes the neotropical genera that Morrison (1955) placed here, plus the genera that he included in the Amphicyclotidae, exclusive of those that are now placed in the Crocidopominae (Thompson, 1967: 15). The subfamily also includes the seven Pacific Island genera discussed by Clench (1949: 4-13) and Solem (1959: 180-184).

The subfamily Neocyclotinae is characterized by possessing a verge that is located on the center of the nape. An open seminal groove extends from the end of the prostate, across the nape, and to the tip of the verge. In some species of one genus (*Neocyclotus*) the groove may be secondarily coalesced to form a sperm duct that is connected to the surface of the verge by a keratinized raphe. This condition is different



TEXT-FIG. 2. Female reproductive systems of two species of Aperostominae. A. *Farcimen croteum* (Gmelin); 2.5 mi. s.w. Yabucoa, Puerto Rico. B. *Farcimen croteum* (Gmelin); enlarged view of seminal receptacle with the receptacle chamber partially opened. The albumen gland has been partially freed from the side of the receptacle. C. *Aperostoma mexicana salleana* (Martens); 4.3 mi. e. Cordoba, Veracruz. Scale for A equals 5 mm; scales for B and C equal 2 mm.

from the sperm duct that occurs in the Crocidopominae, which has a tubular verge without any connecting raphe between the sperm duct and the outer surface. The female system is distinct in possessing a hollow saculate seminal receptacle, an albumen gland that consists of an enlarged segment in a loop of the oviduct, and in having the uterine lumen divided longitudinally into two chambers by an involution. The division is generally incomplete so that a horseshoe shaped cavity is formed in cross-section, but in one genus (*Neocyclotus*) the involution completely divides the lumen except at the distal end of the uterus. A copulatory bursa is absent or is rudimentary and imbedded in the uterine wall.



TEXT-FIG. 3. Diagramatic illustrations of three types of female reproductive systems in the evolution of the Neocyclotinae. A, C, and E are longitudinal sections through the uterus. B, D, and F are cross-sections through the above utera at the points indicated by the arrows, and show the respective degrees of involution of the uterine wall. A. A primitive condition in which the seminal receptacle and the oviduct are separate and discharge on the outer surface of the uterus, as in *Dicrista* new genus. C. A more advanced stage in which the seminal receptacle enters the oviduct, and the genital duct terminates at the end of the vagina, as in *Amphicyclotus*. E. A highly modified stage in which the genital duct enters the uterus prior to the vagina. The uterine lumen is completely divided by an invagination so that a single sigmoid passage occurs through the uterus from the genital duct to the vagina.

Evolution within the subfamily involved various elaborations of the terminal structure of the verge and modification of the female reproductive system. Features of the shell and the operculum have no relationship to underlying anatomical changes. Suprageneric categories based upon conchological characters are without basis, for several prominent external features occur independently throughout the subfamily (color patterns, siphonal notches, calcified opercula, etc.).

In the primitive condition the seminal receptacle has a long slender duct that is independent of the oviduct throughout its length and both ducts discharge on the outer surface of the uterus above the vagina (Text-fig. 3, A). In more advanced stages the receptacle duct discharges into the oviduct, forming a common genital duct below their union, and the genital duct terminates at the vaginal opening (Text-fig. 3, C) or into the terminal segment of the uterine lumen (Text-fig. 3, E).

Among the Middle American genera *Dicrista* new genus possesses the most primitive condition, (as in Text-fig. 3, A-B) which is only slightly modified in *Xenocyclus* new genus. *Amphicyclotus* (as in Text-fig. 3, C-D) is intermediate in structure between *Dicrista* and *Neocyclotus* (as in Text-fig. 3, E-F). Presumably other American genera are similar to *Neocyclotus*. *Ostodes* Gould and *Gonatoraphe* Mollendorff are the only members among the Pacific island genera that have been investigated sufficiently to indicate the structure of their female reproductive systems (Solem, 1959: 180-184). They too are similar to *Neocyclotus*.

Mexcyclotus lutescens (Pfeiffer)

Cyclostoma (*Cyclophorus*) *lutescens* Pfeiffer, 1851; Proc. Zool. Soc. Lond.: 250.

Cyclophorus lutescens (Pfeiffer), Pfeiffer, 1852; Monogr. Pneum. Viv., 1:82.

Mexcyclotus lutescens (Pfeiffer), Bartsch and Morrison, 1942; Bull. U.S. National Mus., (181): 179 (not 181).

Apparently this is a South American species that has been identified with a form occurring in Mexico. A brief review of its history is given. Pfeiffer (1851: 250) described *lutescens* from Brazil. He subsequently (1865: 69) recorded

lutescens from Panistlahuaca, Oaxaca, on the basis of material collected by Boucard. Fischer and Crosse (1886: 139) included *lutescens* in the Mexican fauna on the basis of Pfeiffer's identification of Boucard's specimens. Angas (1879: 483) recorded the species from the Nicoya Peninsula of Costa Rica. Martens (1890: 7) hesitantly accepted the Costa Rican record and suggested the identity of *Cyclotus cooperi* Tryon from Mexico with *Cyclostoma lutescens* Pfeiffer. Bartsch and Morrison (1942: 181) recognized the two species as distinct, but they included both in the Mexican fauna, and designated a new genus, *Mexcyclotus*, with *lutescens* as the type species. Solem (1956: 55) synonymized *cooperi* with *lutescens*, and discussed its distribution in Mexico and Central America.

Apparently the sole basis for including *lutescens* in the Mexican fauna is Pfeiffer's citation of specimens from Panistlahuaca, Oaxaca. Later authors followed Pfeiffer and credited the identity of the Mexican form to *lutescens*, but at no time did Pfeiffer state that the original locality of Brazil was in error, though implied by von Martens (1890: 7). The identity of Angas's Costa Rican record is also doubtful. Von Martens accepted the locality as probable because it was bracketed by records from Brazil and Mexico, but he did not accept some of Angas's other Costa Rican cyclophorid records (Martens, 1890: 4).

An important distinction between *lutescens* and Mexican forms, or their identity, depends upon the opercular structure of the type of *lutescens*. All authors on Mexico subsequent to Pfeiffer (1865) assumed that Mexican populations called *lutescens* have an operculum similar to that described for the Brazilian specimens. The types of *lutescens* currently lack opercula (J. F. Peake, personal communication), but some important points are stated in the original description (Pfeiffer, 1851: 250). A translation is given below.

"Shell umbilicate, depressed conical, solid, obliquely threadstriate, silky (shiney), yellowish white; spire low and conical, acute; suture deep, simple; *whorls 4.5*, convex, *rapidly increasing*, last whorl not descending; umbilicus moderate, deep; aperture slightly oblique, broadly ovate; peristome simple, sharp, continuous, narrowly adnate, upper corner weakly angulate. – Operculum membranous, pale horn colored, coarse and spiral [lamella], outer surface deeply concave. – Major diameter 20 mm, minor diameter 15.5 mm, height 12 mm, aperture height 10 mm."

"Habitat in Brazil."

Several critical points are apparent. The shell is more depressed than any Mexican specimens identified as *lutescens* by recent authors. The shell is unusually large, has unusually few whorls, and the *whorls rapidly increase in size* in contrast to Mexican specimens identified as *lutescens*. The operculum is described as being rough and membranous, not calcified. Similar observations on the operculum were made by von Martens (1890: 2) and Kobelt (1902: 254) who had both examined Pfeiffer's types. Kobelt merely stated that the operculum was membranous and tightly coiled.

All authors subsequent to Pfeiffer assumed that Mexican specimens identified as *lutescens* have a membranous operculum as described by Pfeiffer. Actually they do not. The Mexican forms all have a well developed oblique calcareous lamella in addition to a chitinous lamella. The differences in opercular structure between *lutescens* and *cooperi* precludes their specific or generic identity. Because of these differences the name *Mexcyclotus* must be restricted to the "Brazilian" species (*lutescens*), and the Mexican species (*cooperi* and others) must be placed in a separate genus described below.

Even if we assume that the original locality given for *lutescens* was in error, but that the name applies to a Mexican species and that Pfeiffer omitted important points in his description of the operculum, the name cannot be clearly identified with any Mexican form, for Pfeiffer's description fails to mention characteristics of the embryonic sculpture which would be necessary to restrict the name among known taxa.

Dicrista new genus

TYPE SPECIES: *Dicrista liobasis* new species.

A neotropical genus of cyclophorid snails superficially characterized by the combination of characters of its shell and operculum, and more fundamentally by the characters of the male and female reproductive systems. The shell is variable in size and shape. It is usually helicoid or depressed helicoid; occasionally very depressed. The shell has about five whorls at maturity. The whorls slowly increase in size. The umbilicus is variable in size, but always less than 0.30 times the major diameter. The sculpture is simple, consisting of axial threads or riblets. In some instances the axial sculpture may be quite heavy and rugose, but it is always simple, and follows the line of growth, not anastomosing or oblique or otherwise modified. The axial sculpture may begin on the second embryonic whorl in one group of species or it may

not appear until after the third whorl in another group. The aperture is generally simple, but two species have a small siphonal notch in the upper corner.

The operculum is highly variable within the genus (Pl. I and Text-fig. 4), but always consists of a chondroid basal plate with a calcareous and a chitinous lamella on the outer surface. The basal plate may be simple or it may be laminated with calcareous deposits. The lamella may be simple, oblique, and overlapping, or they may be nearly vertical and highly modified for particular species. The operculum is usually concave in cross section and consists of about nine to ten closely coiled whorls.

The male possesses a stocky, moderately flattened verge that ends in a simple rounded or bluntly pointed tip, and has a small triangular penis on the dorsal surface (Text-fig. 5). The penis lies near the right margin and is reflected posteriorly. A low sigmoid lateral fold lies along the outer margin of the penis. An open seminal groove originates on the side of the nape at the anterior end of the prostate, and continues along the ventral surface of the verge, and back along the inside surface of the lateral fold. The inner wall of the prostate, as in the uterus of the female, is lined with a thick layer of glandular tissue that is involuted mesially to produce a large pendulous glandular fold that divides the prostatic lumen into two cavities that are connected mid-ventrally by a narrow gap.

The uterus is elongate, cylindrical, and of nearly uniform width throughout its length (Text-fig. 6). The interior of the uterus is lined with a thick glandular layer that is involuted mesially to form a large pendulent fold which divides the uterine lumen into two lateral chambers that are interconnected mid-ventrally by a narrow gap. The vagina consists of a small slit located on the columellar side of the anterior end of the uterus, and is continuous with the uterine lumen. The seminal receptacle is a small saculate pouch appressed against the distal end of the uterus. It has a thick brown glandular wall, and *has a simple muscular duct that is split along one side near its base.* The albumen gland consists of a large sigmoid loop in the oviduct. The base of the loop is closely bound by connective tissue to the distal sixth of the uterus. *Both the oviduct and the receptacle duct are partially imbedded in the uterine wall, and terminate just above the vagina beneath a thick fleshy flap on the columellar side of the uterus. The two ducts discharge into separate narrow grooves in the wall of the uterus.* The grooves are parallel to the vaginal slit and are not interconnected.

The genus is known to occur in southwestern Mexico. It questionably has been recorded from Costa Rica. *Dicrista* contains seven known species representing two species groups that are distinguished by the sculpture on the early whorls of the spire. One group, containing the type species, has strong axial ribs on the second embryonic and following whorls. The other group does not develop axial sculpture until after the third whorl. The groups parallel each other in modifications of other characters of the shell and operculum. I consider the typical group with sculptured embryonic whorls to be the most specialized, and derived from the more generalized smooth-whorled stock. Species of the latter group have also undergone a high degree of specialization, but along individual lines and not as a group.

Dicrista and the following genus form an isolated stock that is not closely related to other genera of the subfamily Neocyclotinae, because of the structure of the reproductive systems.

The generic name *Dicrista* is derived from the Latin and refers to the two opercular lamella, one calcareous and one chitinous. The name is of the feminine gender.

Dicrista cooperi (Tryon)

Cyclotus cooperi Tryon, 1863; Proc. Acad. Nat. Sci. Phila., 1863: 281; pl. 2, fig. 2. (Type locality: nr. Mazatlan, Sinaloa).

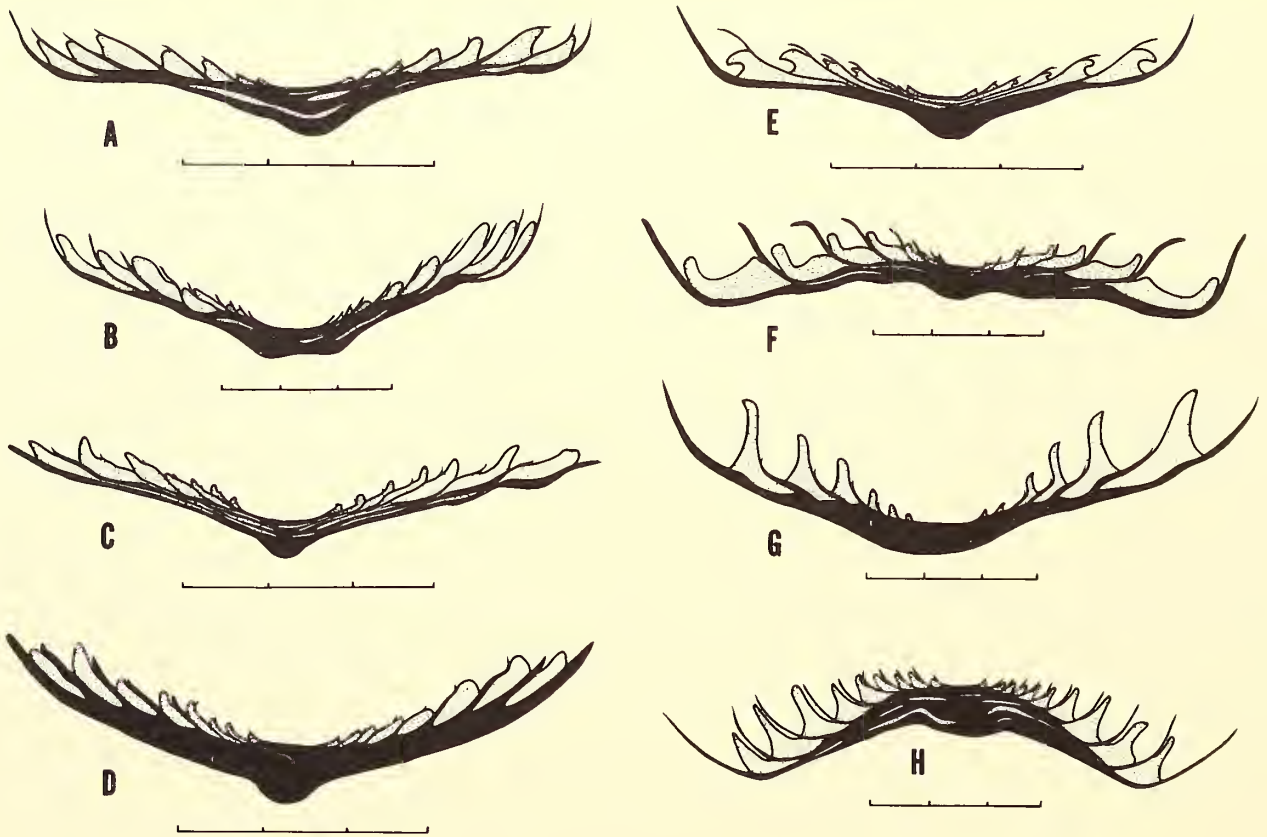
Mexcyclotus cooperi (Tryon), Bartsch and Morrison, 1942; Bull. U. S. Nat. Mus., 181: 180; pl. 24, figs. 10-12.

Mexcyclotus lutescens (Pfeiffer), Bartsch and Morrison, 1942; Bull. U. S. Nat. Mus., 191: 181; pl. 24, figs. 13-15.

Mexcyclotus lutescens (Pfeiffer), Solem, 1956; Proc. Acad. Nat. Sci. Phila., 108: 55-56; pl. 5, figs. 12-13, 16.

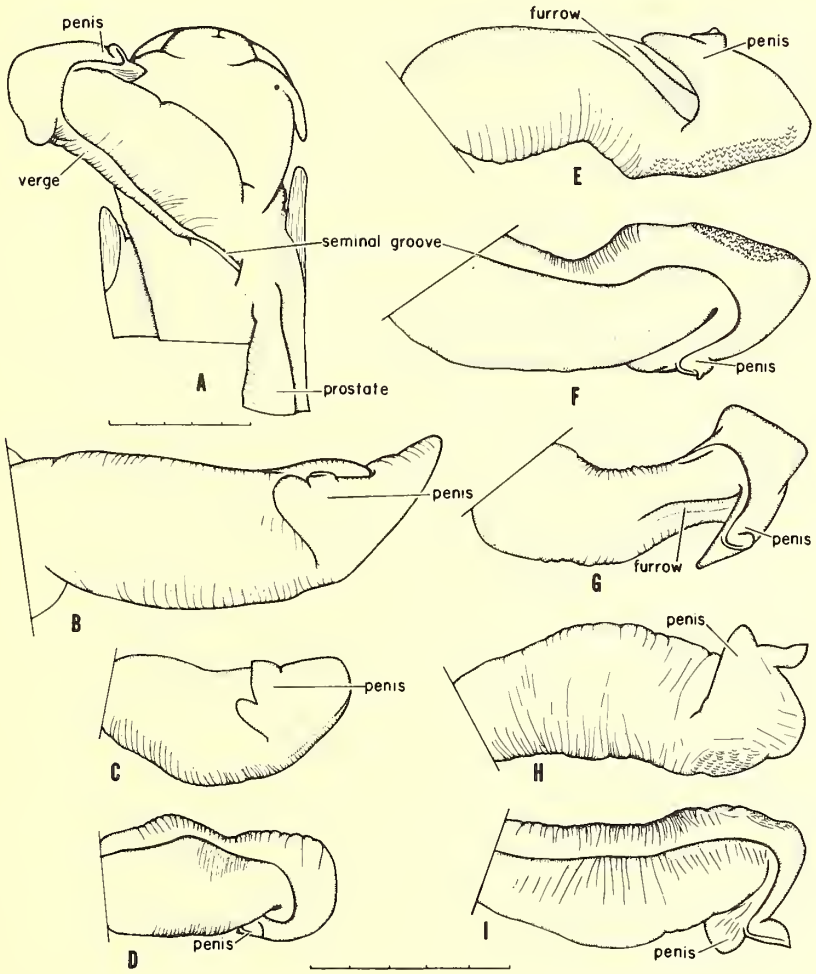
Diagnosis. A species of *Dicrista* allied to *liobasis, damianensis,* and *flavescens,* and distinguished from others by its rugosely sculptured embryonic whorls. It differs from the first three species by its moderately small size, conical shape, closer sculpture on the early whorls, and narrower umbilicus. It approaches *damianensis* in these characters, and may be subspecifically related. The primary differences between the two forms are in the smaller shell, lack of a subsutural chord, and flattened operculum of *cooperi.*

Shell (Pl. II, A-C). Small or medium sized. Solid, but not thick. Helicoid; height 0.67-0.95 times major diameter. (The holotype is unusually depressed. All other specimens examined have a height/width ratio greater than 0.70).

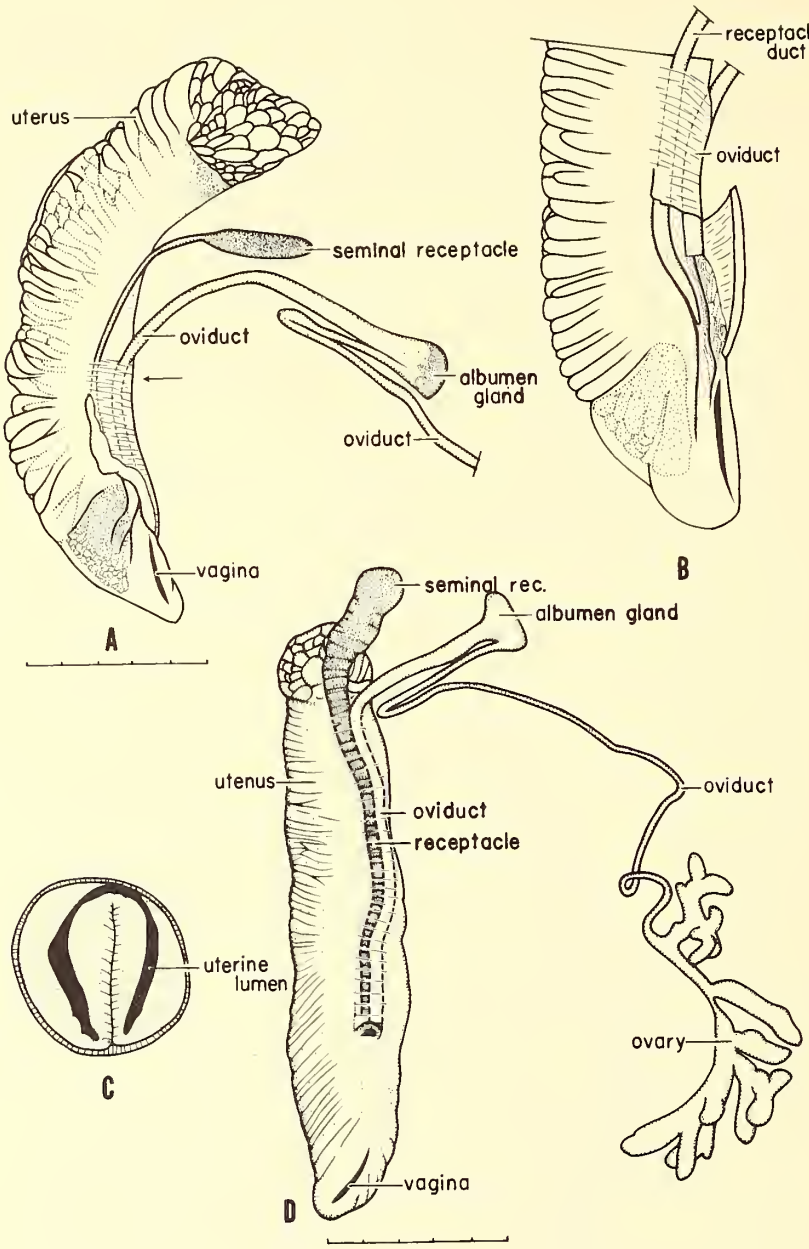


TEXT-FIG. 4. Cross-sections of the opercula of *Dicrista* new genus and *Xenocyclus* new genus. showing relationships between the chitinous lamella (black), and the calcareous lamella (stippled). A. *D. cooperi* (Tryon), 7.6 mi. n.n.e. Manzanilla, Colima (UF 20190). B. *D. damianensis* (Solem), holotype. C. *D. liobasis* new species, paratype (UF 20195). D. *D. flavescens* new species, holotype. E. *D. identatus* new species, paratype (UF 20192). F. *D. petersi* (Solem), holotype. G. *D. rugosa* new species, paratype (UF 20200). H. *X. patulus* new species, paratype (UF 20186). Scales equal 3 mm.

Spire conical, straight-sided or weakly convex. Color dull brown with darker streaks along growth lines. Whorls regularly and relatively slowly increasing in size; minor diameter 0.79-0.83 times major diameter. Whorls uniformly rounded, not shouldered; not noticeably descending near aperture. Suture deeply impressed, without subsutural chord. Umbilicus narrow, 0.16-0.20 times major diameter. Whorls 4.4-5.3 in mature specimens. Embryonic whorls 1.8-2.0; protruding. First embryonic whorl smooth, 0.8 mm. in diameter perpendicular to initial suture. Next embryonic with strong, rugose, oblique riblets. Following whorls with similar riblets that become more closely spaced and less distinct until on last whorl or so the sculpture consists of numerous close, sharp axial threads and striations, which continue only slightly diminished across the ventral surface of the body whorl and into the umbilicus. Aperture circular, slightly higher than wide; 0.45-0.49 times major diameter. Narrowly attached to but not indented by previous whorl. Advanced at the parietal margin; oblique in lateral profile. Parietal callus moderate, opaque. Peristome simple, sharp. Interior of aperture white.



TEXT-FIG. 5. Verges of *Dicrista* new genus and *Xenocyclus* new genus. A. *D. liobasis* new species, dorsal view of head and nape with the verge bent forward to show the seminal groove. B. *D. liobasis* new species, dorsal view of verge. C-D. *D. rugosa* new species, topotype. E-G. *D. flavescens* new species, holotype; G is a view of the right margin of the verge showing the coarse of the furrow under the penis. H-I. *X. patulus* new species, topotype. Scales equal 5 mm; scale under A for that figure only; scale at bottom of page for all others.



TEXT-FIG. 6. A. *Dicrista liobasis* new species, ventral view of uterus and associated organs; topotype. B. *Dicrista liobasis,* enlarged view of lower half of uterus showing terminations of the genital ducts beneath a flap of tissue. C. *Dicrista liobasis,* cross-section of uterus A at point indicated by arrow. D. *Xenocyclus patulus* new species, ventral view of uterus and associated organs, topotype. Scales equal 5 mm.

Measurements in mm of six specimens of *D. cooperi* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
15.8	12.8	12.1	–	7.4	7.1	type
17.5	–	14.0	–	8.2	8.2	ANSP 74555
14.5	–	13.7	–	7.0	6.9	USNM 251718
16.1	12.9	13.2	2.9	7.5	7.5	
15.0	11.8	11.6	3.0	7.1	6.9	
14.0	11.4	11.7	2.2	6.9	6.8	

Operculum (Pl. I, B; Text-fig. 4, A). Consisting of eight to nine whorls in large specimens. Nucleus depressed, forming a low mound on inner surface. Basal chondroid plate partially laminated with calcareous deposits. Chitinous spiral lamella lying at an oblique angle. A narrow, calcareous spiral lamella lies against the underside of the chitinous lamella, and extends nearly as far out as the latter. Outer edge of calcareous lamella simple, though overlapping succeeding whorl.

Specimens Examined. Sinaloa: nr. Mazatlan (ANSP 13019 – type and paratype of *Cyclotus cooperi* Tryon); Rosario (ANSP 74555. 5). Jalisco: Hacienda de Istapa (USNM 251718. 13); San Sebastian (USNM 251717. 1). Colima: 7.6 mi. N.N.E. Manzanilla, 200′ (UF 20190. 8). Guerrero: Zihuatenejo (USNM 517886. 1), (ANSP 194612. 4). Oaxaca: no specific locality (ANSP 13021. 3), (MCZ 136023. 1). Costa Rica: no specific locality (ANSP 13020. 2).

Remarks. Solem (1956: 55) recorded a specimen (ANSP 184033) from near Zihuatenejo, Guerrero. This and two others from nearby localities (UF 20204, UF 20205) are not identifiable as *cooperi* because of their notably heavier and larger shells, but cannot be placed elsewhere because they are weathered specimens that lack sculptural details and opercula.

I am not satisfied that other specimens listed from Guerrero, or those from Oaxaca and Costa Rica, are identifiable with this species or that they represent authentic records. These lots consist of only one or a few specimens, and are unsatisfactory for critical comparison. The specimens cited from Zihuatenejo, Guerrero, (USNM 517886) cannot be satisfactorily identified with or distinguished from *cooperi*. They are mostly immature, broken, and lack opercula. Specimens that bear such locality data as "Oaxaca" and "Costa Rica" defy verification about the authenticity of their data.

The confusion of *cooperi* with *Mexcyclotus lutescens* has been discussed under that species.

Dicrista damianensis (Solem)

Mexcyclotus petersi damianensis Solem, 1956; Proc. Acad. Nat. Sci. Phila., 108; 57-58; pl. 5, fig. 11; pl. 6, figs. 13, 18.

Diagnosis. A species of *Dicrista* related to *cooperi, liobasis,* and *flavescens* by its rugosely sculptured embryonic whorls. It is distinguished by its depressed helicoid shape, narrow umbilicus, the presence of a subsutural chord, its larger size, and its deeply dished operculum.

Shell (Pl. III, D-F). Medium sized. Dull light brown. Moderately thick for genus. Depressed-helicoid, height 0.67 times major diameter. Spire conical; very slightly convex on outline. Whorls regularly increasing in size; minor diameter 0.76 times major diameter. Whorls nearly uniformly rounded, dorsal surface sloping. Umbilicus funicular, 0.20 times major diameter. Last whorl descending near the aperture. Suture deeply impressed, slightly channeled along suture. Subsutural chord very weakly indicated. 4.8 whorls. Embryonic whorls 1.8; raised, but only moderately protruding. First whorl 1.0 mm in diameter; smooth. Following ¾ whorl with strong, widely spaced riblets. Following whorls with coarse thread-riblets that become more closely spaced and less well defined with growth of shell. Thread riblets only slightly diminished in texture on ventral surface of body whorl. Aperture width 0.41 times major diameter. Parietal callus thick, opaque. Peristome simple, sharp, moderately arched along dorsal surface; oblique in lateral profile. Interior of aperture dull white.

Measurements in mm of the holotype of *D. damianensis* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*
20.8	15.7	14.6	4.3	9.1	9.0

Operculum (Pl. I, C; Text-fig. 4, B). Consisting of about 10 closely coiled whorls. Conical; deeply dished in cross-section. Basal chondroid plate weakly laminated with calcareous deposits. Chitinous spiral lamella moderately thin and broken away along its edge. Underlying calcareous lamella moderately thick, oblique, and overlapping so that outer face of operculum is predominantly calcified in appearance.

Type Locality. Michoacan, 1 mile north of San Pedro Damian Naranjestilla (18° 18′ N, 103° 8′ W). Holotype: UMMZ 184837; collected by James A. Peters (only known specimen).

Remarks. This species was described originally as a subspecies of *D. petersi* (Solem). *D. damianensis* differs from *petersi* in so many respects, including the nature of the opercular structure, the absence of a siphonal notch, and the presence of axial sculpture on the second embryonic whorl, that even a close specific relationship is not tenable.

D. damianensis is closely related to *D. cooperi* as is discussed under that species. It is also closely related to *D. liobasis*. It differs from *liobasis* by having a more deeply dished operculum, a narrower umbilicus (about 0.20 times major diameter), a more elevated spire, a more deeply impressed suture, coarser and closer thread riblets on the second and third whorl, having the sculpture continue scarcely diminished across the ventral surface of the body whorl, and by lacking a distinct subsutural chord.

Dicrista liobasis new species

Diagnosis. A species of *Dicrista* related to *cooperi, damianensis*, and *flavescens* because of the costulate sculpture on the embryonic whorls. It is distinguished by its very depressed helicoid shape, its concave spire, its suture which is only moderately impressed, its broad umbilicus, and its narrow aperture. Some of these characters are shared with one or two of the other species, but *liobasis* is distinguished from all by the sculpture on its last whorl. The sculpture consists of thread-striations on the dorsal surface, which become obsolete at the periphery leaving the ventral surface and the umbilicus smooth. The opercular characteristics described below also tend to characterize *liobasis*.

Shell (Pl. III, A-C). Medium sized. Moderately thin. Very depressed helicoid; height 0.58-0.63 times major diameter. Spire concave. Color light brown with slightly darker radial streaks due to periostracal fringes on the ribs. Suture moderately impressed. A moderate subsutural chord is present. Umbilicus broadly open, 0.25-0.29 times major diameter. Whorls regularly increasing; minor diameter 0.72-0.78 times major diameter. Whorls nearly uniformly rounded, slightly flattened dorsally. Body whorl descending slightly near the aperture. Whorls 4.6-5.0 in large specimens (4.7 in holotype). Embryonic whorls 1.7; protruding so that spire is concave in outline. Diameter of first whorl 0.9-1.0 mm perpendicular to initial suture. First whorl smooth; following ¾ whorl with strong uniform, widely spaced thread-riblets that are most developed along the upper suture. Following two whorls with uniformly spaced thread-riblets that become more closely spaced on the body whorl. Thread-riblets with low periostracal fringes. About ¾ riblets/mm on penultimate whorl. Thread-riblets becoming obsolete below periphery of body whorl. Ventral surface and umbilicus smooth and shiny with incremented striations. Aperture subcircular, usually slightly higher than wide; narrowly attached to preceding whorl. Aperture 0.40-0.43 times major diameter. Parietal region slightly advanced, thick, weakly translucent. At the most the aperture is only slightly indented by the previous whorl. Peristome simple, slightly arched forward above periphery; moderately oblique in lateral profile. Interior of aperture dull white.

Measurements in mm of seven specimens of *D. liobasis* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
22.1	16.6	12.9	6.0	9.1	9.3	holotype
21.4	15.8	13.4	6.0	8.7	8.5	paratype
21.7	16.1	12.8	6.3	9.2	8.9	paratype
22.1	16.0	13.4	5.5	9.4	9.2	paratype
21.1	16.5	13.3	5.1	9.5	9.1	paratype
20.6	15.6	13.0	5.7	8.1	8.4	paratype
19.0	14.1	11.4	5.2	8.4	8.0	paratype

Operculum (Pl. I, D; Text-fig. 4, C). Consisting of about nine to ten whorls in large specimens. Weakly concave with a central depression. Nuclear region with a small knob on inner surface. Basal chondroid plate thin and interlaminated with thin calcareous deposits. Calcareous lamella paralleling chitinous lamella, but thicker and more resistant so that outer surface of operculum may appear completely calcified. Calcareous lamella deeply implanted into chitinous structure of operculum.

Male. The verge (Text-fig. 5, A-B) originates on the middorsal region of the nape and is ovate in cross-section. When retracted the verge lies under the mantle and is directed posteriorly. The distal end of the verge terminates in a broad but flat triangular point. A triangular penis is folded back along the dorsal surface of the verge and is directed toward the base. The end of the penis is flattened and bluntly rounded. The penis bears along its dorsal margin a smaller fleshy convolution in which the seminal groove terminates. The seminal groove extends the length of the verge. It lies on the ventral surface of the basal half of the verge, and curves along the lateral margin of the penis to where it ends in the lateral fold on the side of the penis.

The verge of this species is characterized by the simple structure of the penis, which lacks any accessory modification, except for the lateral fold. It is also characterized in lacking any papillae, grooves, or other modifications.

Female. The uterus (Text-fig. 6, A-C) is elongate and nearly cylindrical in cross-section. The vaginal slit is confined to the anterior tip of the uterus along the columellar margin, and continues into the uterine lumen. The uterine walls are lined on the internal surface with a thick glandular layer that forms a large pendulous fold that extends nearly across the lumen of the uterus. The fold divides the lumen into two chambers that are interconnected by a narrow gap along the ventral margin, and extends the length of the uterus. The outer surface of the uterus and its distal margin are creased by the arrangement of the internal glandular masses. The anterior end of the uterine wall also contains a small lobate yellow glandular mass that lies lateral and slightly distal to the vaginal slit. The oviduct has an elongate sigmoid loop that forms the seminal receptacle, and is attached at its base by connective tissue to the distal fourth of the uterus. The seminal receptacle contains a small yellow grandular mass in its distal loop. The seminal receptacle lies appressed to the ventral side and distal end of the uterus. It is an elongate saculate structure that is brown in color with a thick glandular wall. The oviduct and the seminal receptacle have separate ducts that extend to the anterior fourth of the uterus where they discharge independently under a thick fleshy flap on the columellar margin. The distal end of the receptacle duct is split along its lateral margin beneath the flap and discharges into a narrow, shallow groove. The end of the oviduct is truncate and discharges into a similar narrow groove that parallels the bursal groove. These two grooves tend to lie parallel to the vaginal slit, and the three structures are not interconnected.

Type Locality. Jalisco, a limestone sink 6.0 miles southwest and 6.6 miles east of Pihuamo; 2000 feet elevation. Holotype: UF 20194; collected 3 August, 1966 by Fred G. Thompson. Paratypes: UF 20195 (13), UF 20196 (11), UMMZ 216546 (4); same locality as the holotype.

The type locality is at the base of a huge limestone sink that lies atop a hill overlooking the valley of the north tributary of the Rio Tuxpan. The vegetation in the area consists of dry scrub forest with little ground cover. Snails were found in debris and leaf mulch around limestone boulders.

Remarks. This species is superficially similar to *D. flavescens*. See the latter species for a discussion of the differences between the two. *D. liobasis* is also similar to *damianensis* (Solem) on the basis of its opercular structure. They are alike in having thin basal plates with calcareous laminations, and with predominate oblique calcareous lamella on the outer surface. They differ as is discussed under *D. damianensis*.

Dicrista flavescens new species

Diagnosis. A species of *Dicrista* related to *liobasis, cooperi*, and *damianensis* because of costulate sculpture on the embryonic whorls. It is distinguished by its yellowish brown color, its depressed-helicoid shape, its sculpture consisting of dense thread-striations that continue undiminished into the umbilicus, its wide umbilicus, its narrow aperture, and its dorsally flattened whorls. The most important characters special to *flavescens* are in the structure of the operculum, which consists of a thick basal chondroid plate lacking calcareous lamination, and possessing thick, resistant chitinous, and calcareous spiral lamella on the outer surface. Features of the verge described below are probably also peculiar to the species.

Shell. (Pl. II, G-I). Medium sized. Moderate in thickness. Depressed helicoid; height 0.67-0.72 times major diameter. Periostracum yellowish brown. Spire uniformly conical. Whorls regularly increasing in size; minor diameter

Measurements in mm of the four specimens of *D. flavescens* comprising the type series are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
18.8	14.3	13.0	4.9	8.0	8.1	holotype
21.2	16.1	13.3	6.0	9.1	8.8	paratype
19.8	14.7	12.5	5.6	8.0	8.0	paratype
18.1	13.3	11.3	5.2	7.7	7.6	paratype

0.74-0.76 times major diameter. Suture deeply impressed. Subsutural chord weakly developed. Whorls nearly uniformly rounded, flattened dorsally. Last whorl not descending near the aperture. Umbilicus funicular, showing all previous whorls; 0.26-0.29 times major diameter. Whorls 4.9-5.1 (5.0 in holotype). Embryonic whorls 1.5. First whorl 0.8-1.0 mm in diameter perpendicular to initial suture; raised; smooth. Following half whorl with uniform, evenly spaced radial riblets. Remaining whorls with numerous close radial threads that bear low cuticular fringes. Radial threads continuous and hardly diminished into umbilicus. Aperture nearly circular; narrowly attached to preceding whorl, which only slightly indents aperture. Parietal callus moderate, glassy, transparent, slightly advanced. Aperture moderately oblique in lateral profile; 0.40-0.43 times major diameter. Peristome simple, sharp, nearly planular. Interior of aperture white.

Operculum (Pl. I, E; Text-fig. 4, D). Consisting of about nine whorls in large specimens. Shallowly dished in cross-section. Nuclear region with a small knob on inner surface. Basal chondroid plate thick, *not interlaminated with calcareous deposits*. Thick chitinous lamella extending obliquely outward and turned nearly vertically upward at its outer edge. Calcareous lamella lying parallel to and along underside of chitinous lamella. Upturned ends of chitonous and calcareous lamella forming a raised spiral ridge on face of operculum.

Male. The verge (Text-fig. 5, E-G) originates on the center of the nape immediately beneath the mantle collar, and when retracted is directed posteriorly and to the left within the mantle cavity. The verge is lanceolate in shape with a slight constriction near its middle, and is narrowly ovate in cross-section. The verge ends in an obtuse point, and has a flat triangular wing-like penis that lies on its dorsal side and is directed back toward the base of the verge. The penis bears a small low lateral fold on its outer margin in which the seminal groove terminates. A deep furrow lies on the dorsal side of the verge and passes obliquely under the penis. The distal left third of the verge bears numerous small conical papillae that occur in a restricted zone on the dorsal and ventral surfaces.

Female. None examined.

Type Locality. Guerrero, 7.8 miles south of Mazatlan; 3500 feet altitude. Holotype: UF 20197; collected 28 June, 1966 by Fred G. Thompson. Paratypes: UF 20198 (3); same data as the holotype.

The type locality lies on a limestone hillside along a ravine cut by a tributary to the Rio Omiltan. The area is rugosely karsted. The vegetation consisted of a lush, dense second growth of shrubs, vines, and small trees. Snails were found in leaf mulch around limestone boulders.

Remarks. This species is similar to *D. liobasis*, but differs from it in numerous respects. The most apparent differences between the two species are in the nature of the shell sculpture, the spire, the suture, and the operculum. *D. flavescens* has a dull luster with very close radial threads bearing cuticular fringes. The threads continue undiminished across the ventral surface of the body whorl and into the umbilicus. *D. liobasis* has more widely spaced fringed thread-riblets on the first four whorls. These transform into irregular cuticular threads on the last whorl. The threads and thread-riblets do not continue across the ventral surface of the body whorl, which is smooth and shiny. The embryonic whorls of *flavescens* are not conspicuously raised, and the spire has a simple, depressed, conical outline. The embryonic whorls of *liobasis* protrude, causing the spire to be concave in outline. The suture of *flavescens* is deeply impressed, due to the more elevated, uniformly conical spire. The suture of *liobasis* is only moderately impressed, due to the flattened, concave spire.

More important, but less conspicuous, are differences in the operculum and the male reproductive systems. The operculum of *flavescens* is strongly concave, and has a thick chondroid basal plate that lacks calcareous laminations. The chitinous lamella is relatively thick and resistant to wear. The calcareous lamella is also relatively thick and erect, and is not deeply implanted into the chitinous structure. The operculum of *liobasis* is depressed-conical in cross-

section, and has a relatively thin basal chondroid plate that is interlaminated with calcareous deposits. The cuticular spiral lamella is thin and weak, and is generally eroded away, leaving a nearly naked calcareous outer surface formed by the thin, oblique calcareous lamella, which is deeply imbedded into the chitinous structure.

The verge of *flavescens* is unique in the genus by possessing minute conical papillae along its distal margin extending beneath the reflected penis flap.

Dicrista indentata new species

Diagnosis. A species of *Dicrista* lacking sculpture on the embryonic and upper whorls of the spire, relating it to *petersi* and *rugosa*. It is distinguished by its small size, its helicoid shape, the presence of a siphonal notch that develops only after growth of the fourth whorl, and a strong subsutural chord. The operculum is distinct within this group of species by its relatively simple laminated structure with oblique calcareous and chitinous lamella. The calcareous lamella is peculiar in that it possesses a spiral groove along its outer margin caused by the overhanging free edge.

Shell (Pl. II, D-F). Small. Moderately thick. Light brown in color. Helicoid; height 0.66-0.84 times major diameter. Spire moderately raised, convex in outline. Umbilicus funicular, showing all previous whorls; 0.21-0.27 times major diameter. Whorls slowly and regularly increasing in size; minor diameter 0.75-0.83 times major diameter. 4.5-5.2 evenly rounded whorls in large specimens (5.0 in holotype). Body whorls slowly descending to the aperture. Suture deeply impressed with body whorl loosely attached to preceding whorl. The loosely attached suture along the last whorl is caused by the progressive growth of the siphonal notch, which does not appear until after the shell has acquired about four or more whorls. A conspicuous subsutural chord is also present along all postembryonic whorls, and lies outside of the subsutural groove along the last whorl. Embryonic whorls 1.5-2.0; protruding. First whorl 0.80-0.95 mm wide perpendicular to initial suture. Embryonic and first postembryonic whorls smooth. Following whorls with regular, fine, slightly rugose ribs that become narrower, sharper, and reduced but distinct on the base and in the umbilicus; about 4-6 ribs/mm on the dorsal surface of the last whorl. Aperture nearly circular; slightly higher than wide. Only slightly or not at all indented by previous whorl. Aperture width 0.42-0.45 times major diameter. Peristome complete across parietal margin, but with a small siphonal notch at the upper corner that is exaggerated by the subsutural chord along its outer margin. Peristome slightly oblique in lateral profile; planular. Interior of aperture dull white.

Measurements of the holotype: major diameter, 16.5 mm; minor diameter, 12.3 mm; height, 11.8 mm; aperture height, 7.1 mm; aperture width, 7.0 mm. The holotype is the largest normal shell examined. Larger specimens are gerontic in form.

Operculum (Pl. I, F; Text-fig. 4, E). Consisting of about nine to ten whorls in large specimens. Center of operculum depressed, forming a low knob over inner surface. Basal chondroid plate thick near middle, interlaminated with calcareous deposits near outer surface. Chitinous spiral lamella extending obliquely outward. Calcareous lamella deposited outside of chitinous lamella and forming a parallel spiral band. Calcareous lamella with a spiral groove along outside margin, formed by overhanging free edge of lamella.

Type Locality: Michoacán, 10.0 miles southeast of San Vicente, 200 feet elevation. Holotype: UF 20191; collected 31 May, 1966 by Fred G. Thompson. Paratypes: UF 20192 (36), UF 20193 (15), UMMZ 216845 (5); same locality as the type.

The type locality lies in low rolling hills that extend out toward the Pacific Ocean as a low limestone range. The vegetation consisted of a submesic forests with little ground cover, except for recently fallen leaves and debris. Snails were collected from around limestone boulders and from under logs and debris.

Remarks. This species is similar in appearance to *cooperi* from which it differs in several respects, most important of which is the embryonic sculpture. In *indentata* the embryonic whorls, as well as the next whorl or two, are smooth. Any sculpture at all consists only of fine, irregular incremental striations. Distinct axial thread-riblets do not appear until after at least the third whorl. In *cooperi* strong regularly spaced-riblets appear on the second embryonic whorl, and continue around the spire where they become closer and finer. The difference in embryonic sculpture place *indentata* and *cooperi* in different species groups. *D. indentata* is also distinct by having a siphonal notch in the parietal margin of the aperture, by having a loosely attached body whorl due to a groove formed by the growth of the siphonal notch, by having a well developed subsutural groove, and by having a spiral groove along the outer side of the calcareous opercular lamella.

D. indentata is similar to *D. petersi* because of the development of a siphonal notch in both species late in the growth of the shell. Besides the

very different structures of the opercula, *indentata* is readily recognized by its small size, narrower umbilicus, and its holicoid shape.

Dicrista petersi (Solem)

Mexcyclotus petersi petersi Solem, 1956; Proc. Acad. Nat. Sci. Phila., 108: 56-57; pl. 5, fig. 9; pl. 6, figs. 14-17.

Diagnosis. A large species of *Dicrista* lacking sculpture on the upper three to four whorls of the spire, relating it to *indentata* and *rugosa*. It is distinguished by its large size, depressed helicoid shape, channeled suture, siphonal notch, and weakly convex operculum with a strong calcareous lamella that has a flat base with its outer margin turned vertically upward along the *succeeding* chitinous lamella. The chitinous lamella is high, strong, resistant to wear, and is weakly sigmoid.

Shell (Pl. IV, A-D). Large; solid. Shell depressed-helicoid; height 0.64 times major diameter. Spire low and straight sided. Color light brown with occasional darker streaks along lines of growth. Umbilicus funicular; 0.30 times major diameter. Suture moderately impressed, and deeply channeled by a groove formed by the siphonal notch. Groove accentuated by a spiral chord along its outer margin. Whorls regularly increasing in size; minor diameter 0.74 times major diameter. Whorls rounded; dorsal surface sloping. Last whorl not descending to aperture. Apparently 5.2 whorls in holotype prior to when apical whorl was lost. Embryonic whorls about 1.75; smooth. Following two whorls also smooth, but with very fine incremented striations that become increasingly stronger. Body whorl sculptured with incremental thread-striations that become increasingly prominent toward the aperture, but are very reduced on the ventral surface and indistinct in the umbilicus. Aperture nearly circular, slightly higher than wide; narrowly attached to preceding whorl. Aperture width 0.39 times major diameter. Parietal callus thin and translucent. A strong siphonal notch indents the upper corner. The siphonal notch is accentuated by a shallow groove along its outer margin inside of the aperture. This groove lies beneath the end of the subsutural chord on the outer surface of the shell. Peristome simple, vertical in lateral profile. Interior dull white.

Operculum (Pl. I, G; Text-fig. 4, F). Consisting of ten whorls. Inner six whorls closely coiled; outer whorls more loosely coiled. Weakly convex with outer margins turned upward. Basal chondroid plate thick; very weakly laminated with calcareous deposits. Nuclear region slightly depressed on outer surface. Chitinous spiral lamella nearly erect, and sigmoid with its edge directed laterally. Calcareous lamella thick and flat with its outer margin turned upward along *succeeding* chitinous whorl. Surface of calcareous lamella with rugose spirally oblique striations.

Type Locality. Michoacán, La Placita (=Sulatillo) (18° 32′ N, 103° 37′ W). Holotype: UMMZ 184836, collected 5-9 July, 1950 by James A. Peters. Paratype: ANSP 194642 (juvenile); same data. Only known specimens.

Remarks. This species is known only from the holotype and an immature paratype. The characteristics used to distinguish the species are consistent in both specimens. Its relationship to *D. indentata* and *D. rugosa* are discussed under those species respectively.

Dicrista rugosa new species

Diagnosis. A large species of *Dicrista* related to *petersi* and *indentata* by lacking costulate sculpture on the upper three to four whorls of the spire. It is characterized by its very depressed helicoid shape, only moderately impressed suture lacking a subsutural channel or chord, light brown color that fades to dirty white on the last half of the body whorl, rugose costulate sculpture on the last whorl, and a simple peristome lacking a siphonal notch. The operculum is characteristic in being moderately concave, with a strong erect calcareous lamella that lies against the preceding chitinous lamella. The chitinous lamella is weak and is generally eroded away leaving a nearly bare calcified outer surface to the operculum.

Shell (Pl. IV, E-G). Large, solid. Shiny. Color light brown, tending to fade to white on last half of body whorl. Very depressed helicoid; height 0.63-0.67 times major diameter. Spire straight-sided or only very slightly concave in outline. Umbilicus funicular, showing all previous whorls; 0.24-0.29 times major diameter. Suture only moderately impressed due to low

Measurements in mm of the holotype of *D. petersi* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*
25.4	18.8	16.2	7.9	11.0	10.0

Measurements in mm of six specimens of *D. rugosa* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
24.8	19.5	15.5	6.1	11.2	10.8	holotype
24.4	18.7	15.5	7.0	10.3	10.2	paratype
22.5	17.8	15.2	5.4	10.1	9.9	paratype
26.8	21.2	17.0	7.4	11.4	11.2	UF 20203
25.7	19.6	16.3	6.9	11.0	10.7	UF 20203
25.0	18.7	15.0	7.2	10.7	10.7	UF 20203

spire. Subsutural chord absent. Whorls regularly increasing in size; minor diameter 0.75-0.79 times major diameter. Last whorl descending near the aperture, particularly in large animals, though the descent may not be conspicuous in specimens with fewer than 4.8 whorls. Whorls nearly uniformly rounded, slightly flattened dorsally. Whorls 4.7-5.3 in large specimens (4.9 in holotype). Embryonic whorls 2.0-2.2; moderately protruding. First whorl 1.0-1.1 mm in diameter. Embryonic whorls smooth. Following two whorls also smooth but with fine irregular incremental striations. Body whorl with irregular rugose ribs that become increasingly strong near the aperture, but are poorly defined on the ventral surface, and indistinct in the umbilicus. Aperture circular, slightly higher than wide; narrowly attached to but not indented by preceding whorl. Aperture width 0.42-0.46 times major diameter. Parietal callus moderate and opaque. Peristome simple, oblique in lateral profile. Interior of aperture white.

Operculum (Pl. I, H; Text-fig. 4, G). Consisting of about eight whorls in large specimens. Moderately concave in cross-section. Nuclear region thick, but without knob on inner surface. Outer surface with thick high vertical calcareous spiral lamella that is partially lined on its inner surface by a thin chitinous lamina which generally is eroded away. Outer side of calcareous lamella concave. Basal chondroid plate thick, without calcareous lamination.

Male. The verge (Text-fig. 5, C-D) originates on the center of the nape immediately beneath the mantle collar. The verge is stocky and narrowly ovate in cross-section with a bluntly rounded tip. The penis consists of a small lobate flap, and a larger acuminate lateral fold along the outer margin. The seminal groove terminates on the inner side of the acuminate lateral fold.

Female. None examined.

Type Locality. A small limestone knoll 11.4 miles east of Colima, Colima; 1800 feet altitude. Holotype: UF 20199; collected 28 May, 1966 by Fred G. Thompson. Paratypes: UF 20200 (11); same data as the type.

Other Specimens Examined. Colima: hill 10.0 mi. S. Colima (UF 20201. 5), (UF 20202. 2); 11.4 mi. S. Colima (UF 20203. 16). These specimens are all dead and bleached shells, some of which retain partially deteriorated opercula. They are like the type specimens in size, shape, sculpture, and opercular characters, except that the last series of specimens (UF 20203) tends to be more depressed. The specimens examined for anatomical studies were from the type lot.

Remarks. This species is distinct within the genus because of its large size, smooth sculpture on the spire, and rugose sculpture on the body whorl. It is similar to *D. petersi* (Solem) on the basis of its size, smooth spiral whorls, and calcareous lamella of the operculum, but differs from that species by lacking a siphoral notch and a channeled suture, and by having rugose costulate sculpture on the body whorl. *D. petersi* has a well-developed siphonal notch that forms a subsutural groove, which in turn is accentuated by a raised spiral chord along its outer margin. The sculpture on the body whorl consists of incremental thread striations. In *D. rugosa* the operculum is concave, laminated, and the calcareous lamella is erect along the *preceding* chitinous lamella. In *D. petersi* the operculum is convex, unlaminated, and the calcareous lamella has a flat base with its outer margin erect along the *succeeding* chitinous lamella. *D. rugosa* also differs from *D. petersi* by having a slightly smaller aperture and a slightly wider umbilicus.

Xenocyclus new genus

Type Species: *Xenocyclus patulus* new species.

A neotropical genus of cyclophorid snails closely related to and derived from *Dicrista*, but having so many peculiar features that it warrants separate generic status. The shell is moderately large and depressed dome-shaped. The umbilicus is very wide, being one third or more the major diameter of the shell. The whorls are of correspondingly small caliber and slowly increase in size, with five or more whorls in adult specimens. The sculpture consists of fine

thread striations on the lower whorls. In the only known species the sculpture is obsolete on the ventral surface and absent in the umbilicus. The most distinctive feature of the genus is the presence of a deep, narrow tear-shaped siphonal notch in the upper corner of the peristome. The notch is not open dorsally, but continues back along the suture as a siphonal tube that is nearly completely enclosed, being narrowly open only along the suture of the earlier whorls. The siphonal notch and resulting siphonal tube begin with the first postembryonic whorl.

The operculum (Pl. I, A; Text-fig. 4, H) is similar to some species of *Dicrista*, except that it is an even more elaborate modification than that which occurs on *D. petersi* and *D. rugosa*. The operculum is strongly convex in cross-section, consisting of about 12 tightly coiled whorls. The outer surface bears a nearly vertical calcareous lamella and a slightly higher chitinous lamella that are free from each other.

The male reproductive system is similar to that of *Dicrista*. The verge (Text-fig. 5, H-I) originates on the center of the nape, and has an open seminal groove that runs from the end of the prostate, across the nape and along the verge to its tip. The end of the verge has a simple triangular penial flap reflected posteriorly with the seminal groove terminating in a small lateral convolution.

The female reproductive system (Text-fig. 6, D) is similar to that of *Dicrista* and other neocyclotids, but is peculiar in having a segmented, glandular seminal receptacle duct that has a narrow central lumen. Both the receptacle duct and the oviduct discharge through a single small pore on the outer surface of the uterus about one fifth of the length of the uterus above the vaginal slit.

The genus is monotypic and is currently known from a single locality in the coastal limestone ranges of Colima.

The generic name is derived from the Greek ξένος, meaning strange and κυκλος, meaning circular, or more exactly its affinities with the cyclophorid snails. The name *Xenocyclus* reflects the strange combination of siphonal and opercular characters. The name is of the masculine gender.

Xenocyclus is closely related to *Dicrista*. It is separated because of its highly developed and closed siphonal notch and tube, depressed dome-shaped shell, strongly convex operculum with 12 whorls, and segmented glandular seminal receptacle duct that opens through the same pore as does the oviduct. *D. petersi* might be considered intermediate between the two genera because of its open siphonal notch, deep groove along the suture, and weakly convex operculum, but I am disposed to regard these as independent evolutionary trends. The development of a siphonal notch is a rather plastic character among neotropical cyclophorids. It is highly variable within genera (*Aperostoma, Tomocyclus,* and *Incidostoma*) and similar structures may develop independently even among closely related forms (*Tomocyclus simulacrum* and *T. gealei*). Thus, the similarities between *D. petersi* and *X. patulus* do not necessarily reflect phylogenetic affinity. Other features of the shell and operculum suggests that *D. petersi* is much closer in its relationships to non-siphonate forms of *Dicrista*. The numerous differences between *Xenocyclus* and *Dicrista* indicate an extensive evolutionary transition of *Xenocyclus* from the primitive dicristid lineage.

Xenocyclus patulus new species

SHELL (Pl. V, A-D). Medium to large. Solid but not particularly thick. *Depressed dome-shaped.* Spire slightly raised above last whorl; more elevated in old and gerontic specimens. First embryonic whorl elevated, rapidly increasing in size. Following half whorl constricted and depressed with succeeding whorls being nearly planular. Height 0.53-0.65 times major diameter. Shiny. Color light brown with lighter and darker streaks that parallel growth lines. Nuclear whorls when present nearly white. *Umbilicus very wide,* 0.33-0.38 times major diameter. *Whorls of small caliber,* slowly increasing in size; minor diameter 0.75-0.84 times major diameter. Whorls nearly uniformly rounded; dorsal surface somewhat flattened and sloping. Last ½ whorl descending rapidly to the aperture. Suture very shallow; *partially interrupted by a nearly completely covered siphonal tube that parallels the suture. Siphonal tube formed by a deep narrow tear-shaped siphonal notch in the upper corner of the peristome.* It begins in the first postembryonic whorl and continues uninterrupted to the aperture. The tube is not completely sealed over, but is narrowly open along some portions of the suture, particularly along the upper whorls. Whorls 5.0-5.3. Embryonic whorls 1.5-1.7, smooth, generally broken away. First whorl 0.9-1.0 mm wide perpendicular to initial suture. Whorls of spire nearly smooth, sculpture with fine irregular incremental striations that become progressively stronger and closer. Last 1.5 whorls with numerous close incremental thread-striations that are recurved along the suture, are very much reduced in texture on the ventral surface, and are obsolete in the umbilicus. Aperture nearly circular, slightly higher than wide; *width 0.35-0.39 times major*

Measurements in mm of five specimens of *X.patulus* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
24.0	18.2	13.0	9.1	8.8	8.6	holotype
24.9	19.4	13.7	9.6	10.1	8.7	paratype
23.7	19.0	13.6	8.2	9.2	8.5	paratype
23.2	19.5	14.8	7.4	10.0	9.2	paratype (gerontic)
22.5	17.5	13.5	8.2	9.1	8.7	paratype

diameter. Peristome simple, sharp, complete except for a deep, narrow, tear-shaped siphonal notch at the upper corner. Siphonal notch not open dorsally, but continuing back along suture as a siphonal tube. Upper-outer margin of peristome arched forward. Parietal callus thin, opaque. Interior of aperture white, with a slightly livid tinge.

Operculum (Pl. I, A; Text-fig. 4, H). Consisting of about 12 closely coiled whorls in large specimens. Basal condroid plate convex, with outer lamellar fringe turned upward. Chondroid plate with some small calcareous lenticular deposits. Nuclear region forming a low mound on inner surface. Chitinous lamella turned nearly vertically upward and forming a spiral fringe free from underlying calcareous lamella. Calcareous lamella thick at base and tapered upward; weakly imbedded into chitinous structure.

Male. The verge (Text-fig. 5, H-I) originates on the center of the nape beneath the mantle collar, and when relaxed is directed posteriorly and to the left within the mantle cavity. The verge is dorso-ventrally compressed and is about thrice as long as wide. The distal end is bluntly rounded and bears a triangular flap-like penis that is folded back on the dorsal surface along the right margin. The penis bears a thin fleshy lanceolate appendage on its outer margin. The distal fourth of the verge has a small zone of low rippled papillae along its left margin. The verge has many fine parallel creases elsewhere along the margins. An open seminal groove originates on the side of the nape at the end of the prostate, and extends along the ventral surface of the verge to the lateral appendage on the penis where it terminates. The interior of the prostate, as in the uterus of the female, is lined with a glandular layer along its sides. The glandular layer is involuted mesially to form a large pendulous fold that divides the lumen into two lateral chambers that are connected mid-ventrally by a narrow gap.

Female. The uterus (Text-fig. 6, D) is elongate-cylindrical and of nearly uniform diameter throughout its length. The outer surface is marked by numerous parallel creases that follow the pattern of the underlying glandular masses. The interior of the uterus is like that of *Dicrista*. The sides of the lumen are lined with a thick layer of glandular tissue that is involuted mesially to form a thick pendulous glandular fold that divides the lumen into two lateral chambers which are connected mid-ventrally by a narrow gap. The vaginal slit is located at the anterior end of the uterus and is continuous with the uterine lumen. The seminal receptacle consists of a small brown sac that is appressed against the end of the uterus. The receptacle walls consist of a thick glandular layer of tissue that extends the length of the duct as a weakly segmented glandular stalk with a narrow flat lumen. The albumen gland consists of a large sigmoid loop in the oviduct. The base of the loop is closely bounded by connective tissue to the distal sixth of the uterus. The loop is flattened and laterally expanded to form a saculate albumen gland. Both the oviduct and the receptacle duct are partially imbedded in the uterine wall, and discharge through a single pore that consists of a lobate fold on the side of the uterus and is located about ⅓ of the length of the uterus above the vaginal slit. The ovary consists of a few large digitiform and weakly dendritic glandular clusters.

Type Locality. Colima, a collapsed limestone ridge 0.3 miles southeast of Tamala; 500 feet altitude. Holotype: UF 20185; collected 2 August, 1966 by Fred G. Thompson. Paratypes: UF 20186 (7), UF 20187 (7), UF 20188 (10), UMMZ 216547 (3); same locality as the holotype.

The type locality is a collapsed limestone ridge consisting of large blocks and boulders of limestone. The vegetation along the ridge consists of an open xeric scrub forest that lacks ground cover. Snails were found around the bases of limestone boulders in damp leaf mulch. This is the same locality and station as that from which I collected a new genus and species of helicinid snail, *Ceochasma phrixina* (Thompson, 1968).

Remarks. This species is immediately distinguished from all other neotropical cyclophorids by the presence of a nearly completely closed siphonal tube along the suture. It is also distinguished by its large size, depressed shape, large umbilicus, and strongly convex operculum with 12 whorls. As striking as are these features, relationships are not obscured.

Amphicyclotus Crosse and Fischer, 1879

Amphicyclotus Crosse and Fischer, 1879; Journ. de Conchyl., 27:46. – Bartsch and Morrison, 1942; Proc. U. S. Nat. Mus., 181:183-184. (Type species: *Cyclostoma* (*Cyclophorus*) *boucard:* [Salle] Pfeiffer, 1856).

Amphicyclotus as used in this paper includes only the typical group related to the type species, *A. boucardi* (Pfeiffer). The genus may also include *Megacyclotus, Barbacyclus,* and *Calacyclotus* as subgenera or lesser categories (Solem, 1956: 43; see also Bartsch and Morrison, 1942: 175-186 for definitions of these generic groups). A discussion of the status of these groups is beyond the limitations of the anatomical material currently available. The shell characters used to separate them are distinctive enough to allow consistent recognition, but the emphasis placed on these characters is subjective. Problems of relationships cannot be resolved until anatomical studies are made of the last three "genera."

In the course of this study I have examined the anatomies of three species of *Amphicyclotus.* The species show a surprising degree of diversity in some aspects of the female reproductive system, but in other aspects of both male and female systems they show a degree of uniformity that is characteristic for the genus.

The prostate (Text-fig. 7, C) is relatively simple, with a narrow lumen that forms a broad U caused by a thick glandular ridge along the columellar margin. The verge (Text-fig. 7, A-B; Text-fig. 8) is located on the center of the nape beneath the mantle collar. It is dorso-ventrally flattened, and is directed posteriorly with its distal end recurved anteriorly. The tip of the verge has a funicular tip through which the seminal groove terminates. A moderate bulge is located along the inner margin of the tip of the verge. The bulge and the funicular tip form the penis. An open seminal groove extends from the end of the prostate, diagonally across the nape and along the verge to the tip of the penis.

The uterus (Text-fig. 9) is elongate-fusiform, and has a narrow U-shaped lumen divided by a thick glandular pendulent fold. The vagina consists of a slit in the anterior third of the uterus. The oviduct and the seminal receptacle have a common duct along the columellar margin of the uterus. The duct has an open groove extending its length and terminates at the vagina. The duct is partially imbedded in the uterine wall and has a small saculate vestibule at its distal end. The seminal receptacle consists of a series of convoluted tubules that usually forms a compact mass on a short duct, but may be imbedded in the wall of the vestibule. The oviduct enters the common duct either at its end on the vestibule, or near the middle of the duct (Text-fig. 10). The oviduct forms a sigmoid loop near the end of the uterus. The distal bend of the loop is enlarged into a saculate albumen gland.

Amphicyclotus is distinguished anatomically by the nature of the common genital duct and the seminal receptacle. Close relationships to other genera are not indicated. The genus appears to be a Middle American assemblage of species that is characteristic of the Chiapas-Guatemala-Honduras region, with some species occurring in adjacent areas of Veracruz and Oaxaca. Evolution within the genus appears to have centered about modifications of the female reproductive system, and secondarily about shell characters. For this reason it is difficult to discuss the phylogeny of species that are known only from shells, for similarities of external characters frequently are not substantiated by anatomical data.

Amphicyclotus t. texturatus (Sowerby)

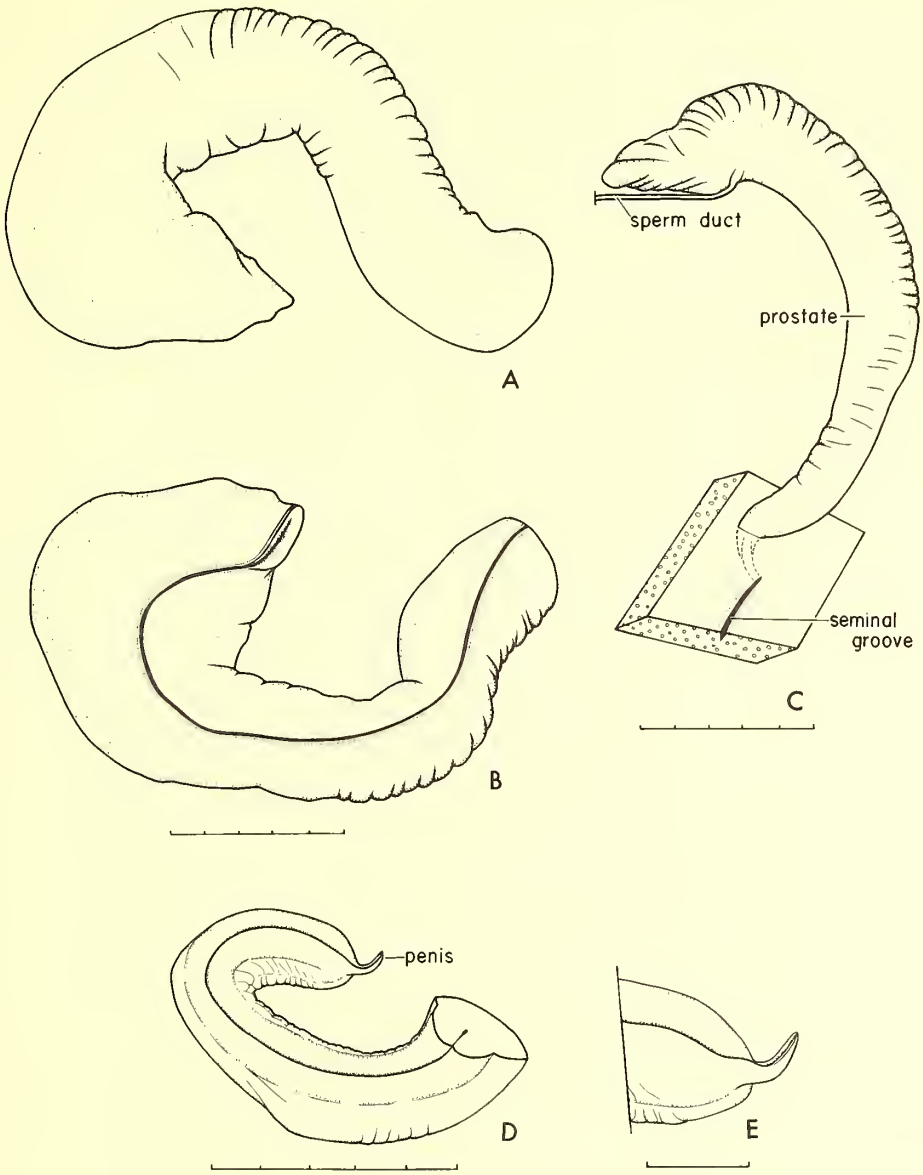
Cyclostoma texturatus Sowerby, 1850; Thesaurus Conchyliorum, Suppl.: 160; pl. 31A, fig. 303. (Type locality: Guatemala)

Amphicyclotus texturatus (Sowerby); Fischer and Crosse, 1880; Miss. Sci. Mex. et dans l'Ameriq. Cent., vol. 2, pt. 7; pl. 35; figs. 2-2b. – 1886, *ibid.;* 144. – Bartsch and Morrison, 1942; Bull. U. S. Nat. Mus., 181:186; pl. 24, figs. 1-3. – Solem, 1956; Proc. Acad. Nat. Sci. Phila., 108:45.

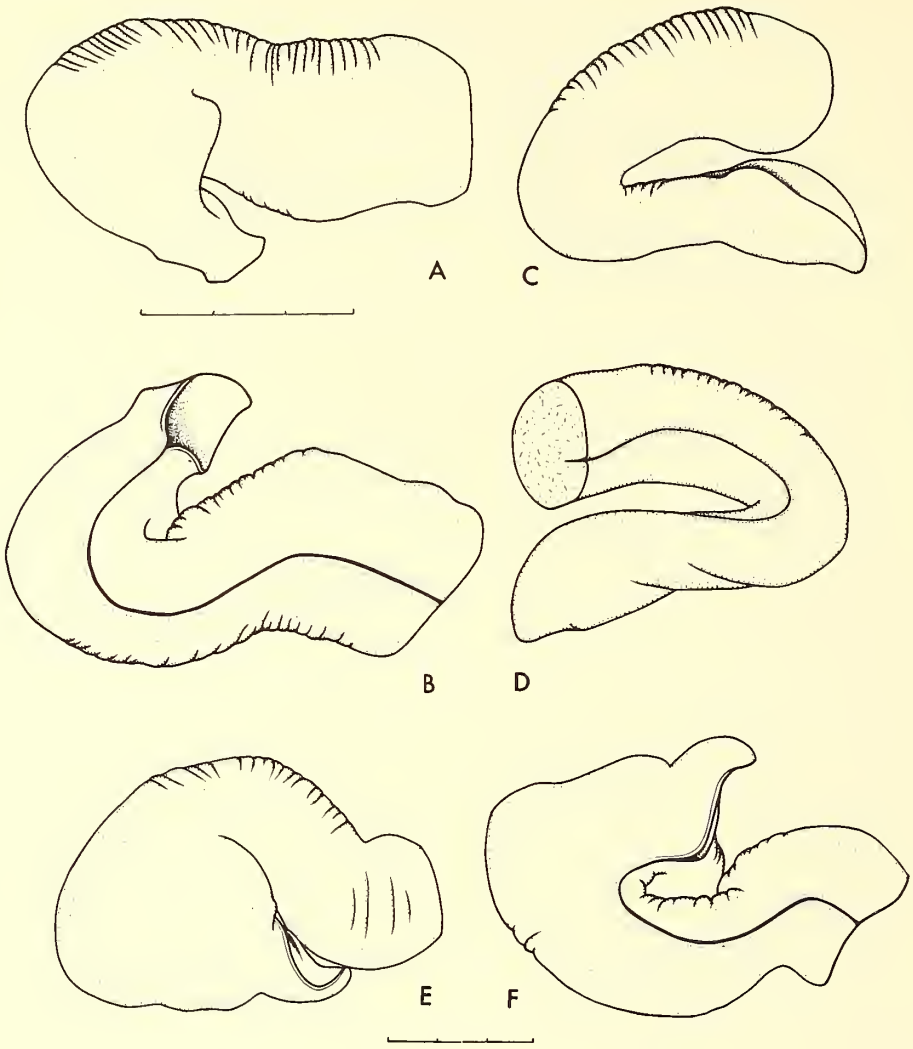
Cyclophorus (*Amphicyclotus*) *texturatus* (Sowerby), Martens, 1890; Biol. Cent. Amer.: 6.

Type Locality. Herein restricted to Cobán, Alta Verapaz, Guatemala.

Guatemala (Dept. Alta Vera Paz): Finca Chichen (UMMZ 149481. 1); Finca de la Providencia (UMMZ 86029. 1); 3 km. W. Finca Samac (UMMZ 132316. 1). No Specific Locality: (UMMZ 86033. 1), (UMMZ 86034. 1), (UMMZ 86644. 1), (UMMZ 35762. 1).



TEXT-FIG. 7. Male reproductive structures of *Amphicyclotus* and *Barbacyclus*. A-C. *A. t. spiralis* new subspecies, topotype. A, B. Dorsal and ventral views of verge. C. Prostate and associated structures. D. *B. princeps* (Pilsbry), ventral view of the verge. E. *B. princeps* (Pilsbry) an enlargement of the distal portion of the verge and penis. Scales for B-D equal 5 mm; scale for E equals 1 mm.



TEXT-FIG. 8. Verges of three species of *Amphicyclotus* showing dorsal (A, C, E) and ventral (B, D, F) views. A-B. *A. parvus* Thompson, paratype. C-D. *A. megaplanus* Morrison. E-F. *A. paulsonorum* new species, topotype. Scales equal 3 mm; scale for A also for B-D; scale at bottom for E and F.

Measurements in mm of seven specimens of *A. t. texturatus* are included so that this subspecies can be compared with the following new subspecies:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	*Cat. No.*
29.4	21.1	17.3	7.6	8.3	7.9	149481 (imm.)
45.1	30.5	22.4	12.8	16.9	19.7	86029
37.8	26.5	21.1	11.2	15.6	15.5	132316
39.1	28.0	19.7	12.0	15.8	16.8	35762
36.8	26.4	19.2	11.3	15.0	15.1	86033
36.7	26.8	20.6	10.2	14.8	15.0	86034
35.8	24.6	20.0	9.6	15.0	16.0	86644

Ratios are: minor diameter, 0.68-0.73 times major diameter; height, 0.50-0.59 times major diameter; umbilicus, 0.27-0.31 times major diameter; aperture width, 0.41-0.45 times major diameter.

A specimen that Solem (1956: 45) recorded from Chiquihuite, Mt. Tacaná, Chiapas, 6400 ft. (UMMZ 144244) does not belong to this form, but represents an undescribed species, characterized by its nearly smooth sculpture and small size. The specimen is insufficient for a taxonomic description.

Amphicyclotus texturatus spiralis

DIAGNOSIS. A form assumed to be subspecifically related to *A. texturatus* (Sowerby). It differs from *texturatus* by being smaller and by having light spiral bands in the periostracum. *A. t. texturatus* is unicolored. Since the anatomy of *A. t. texturatus* is unknown it is not possible to comment further on the degree of differentiation of the two forms.

SHELL (Pl. VI, A-C). Moderately large. Light brown with a rose tinted apex and with light spiral bands, particularly along the periphery. The bands differ in width and are irregular in number. Some are always conspicuous along the periphery and additional ones are clearly evident below the periphery. The bands are weakly impressed as spiral lines into the vermiculate sculpture. Generally depressed helicoid, although some specimens may be nearly planular; height of shell 0.59-0.70 times major diameter. Spire weakly concave in outline. Whorls regularly increasing in size, minor diameter 0.71-0.78 times major diameter. Umbilicus funicular, moderate, 0.24-0.28 times major diameter. Suture impressed, but not channeled. Last whorl descending slightly near the aperture. Whorls 5.2-5.5 (5.5 in holotype). About 2.2 embryonic whorls; moderately raised, rounded, and with a weakly impressed suture. First 1.7 embryonic whorls smooth; following half whorl with weak axial ribs that are most distinct along the suture. The axial ribs continue onto the following whorls, where they become stronger and tend to become vermiculate on the third whorl. Remaining whorls with distinct but relatively weak vermiculating sculpture that extends from the suture to the umbilicus, where it becomes slightly weaker. Vermiculations not conspicuously interrupted by spiral bands in fresh specimens. Aperture circular, oblique in lateral profile; 0.42-0.47 times major diameter. Posterior corner of aperture advanced. Peristone slightly thickened and weakly reflected; connected across parietal wall by a thick callus.

The type series encompasses nearly all variation in size and proportions seen among other individuals.

OPERCULUM. Typically amphicyclotid, consisting of about nine chitinous whorls that weakly overlap. The operculum is deeply dished, with the nuclear region being slightly more depressed.

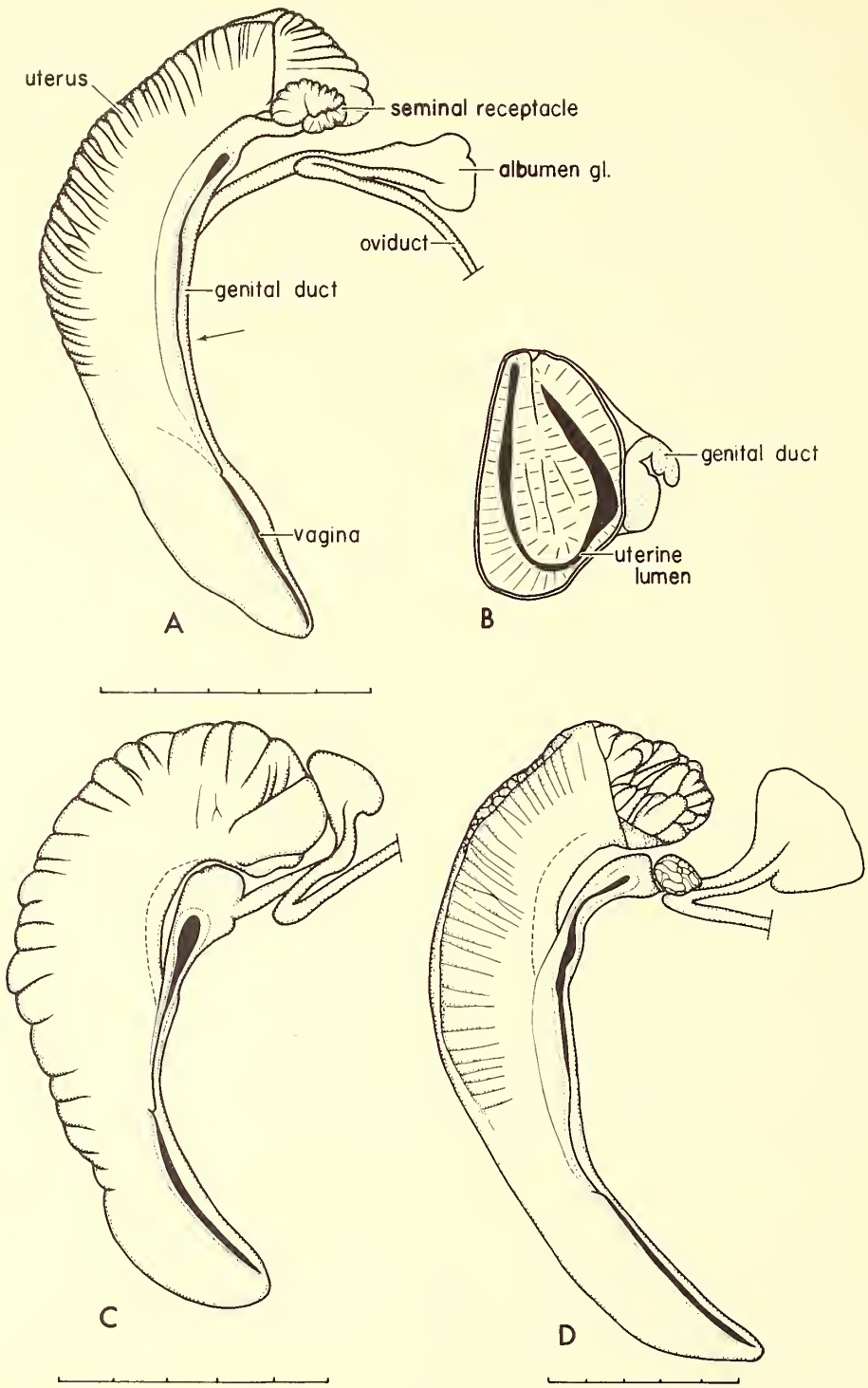
MALE (Text-fig. 7, A-C). The prostate is subtriangular in cross-section and is elongate-tapered with its distal end flattened and wedge-shade. The seminal duct enters the prostate at the base of the wedge-shaped distal segment. The seminal duct discharges directly into the prostatic lumen, which is U-shaped because of a thick glandular ridge along the columellar side of the lumen. The anterior end of the prostate is partially imbedded in the body wall, and opens into a genital groove on the side of the nape.

The verge is located on the center of the nape beneath the mantle collar and is folded posteriorly with its tip reflected anteriorly. The verge is long and ponderous, with its distal end broadly expanded and then tapering to a pointed funicular tip. A small inconspicuous bulge occurs on the right margin near the end of the verge. The bulge and the funicular tip are homologous to the penis of *Dicrista*. An open seminal groove extends obliquely across the nape of the base of the verge and follows a mid-course along the ventral surface of the verge to its funicular tip.

FEMALE (Text-fig. 9, D). The uterus is elongate-fusiform with an expanded, flattened distal end and a narrower, attenuate base. The

Measurements in mm of the six specimens comprising the type series of *A. t. spiralis* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
32.0	23.5	19.2	7.8	14.0	15.0	holotype
33.2	23.3	—	8.9	14.1	14.6	paratype
30.4	21.7	17.9	8.5	13.2	12.8	paratype
29.6	21.7	18.7	7.3	12.9	13.4	paratype
28.9	21.0	17.8	7.2	12.5	13.3	paratype
27.8	21.5	19.6	7.2	12.8	12.0	paratype



TEXT-FIG 9. Female reproductive systems of three species of *Amphicyclotus*. A. *A. paulsonorum* new species, topotype. B. Cross-section of uterus of A at point indicated by arrow. C. *A parvus* Thompson, paratype. D. *A. t. spiralis* new subspecies, topotype. Scales equal 5 mm.

uterine lumen is divided longitudinally by a thick pendulous fold of glandular tissue that is involuted from the columellar margin. The vagina is about one-third the length of the uterus and enters the lumen along the ventral base of the internal glandular fold. The oviduct and the seminal receptacle duct form a common genital duct along the columellar margin of the uterus (Text-fig. 10, C). The duct is partially imbedded in the uterine wall and has an open slit extending from near its apex to the vagina. The apex is slightly enlarged and forms a small vestibule into which the receptacle and the oviduct discharge independently. The oviduct forms a sigmoid loop that is bound by connective tissue to the distal sixth of the uterus. The distal end of the loop is broadly expanded and forms a large saculate albumen gland. The seminal receptacle has a short duct and consists of a series of convoluted tubules that are bound by connective tissue into a small ball.

Type Locality. A coffee grove 4.7 miles north-northeast of Huixtla, Chiapas; 600 feet elevation. Holotype: UF 20176; collected 23 July, 1966 by Fred G. Thompson. Paratypes: UF 20177 (5); same data as the holotype.

Other Specimens Examined. Chiapas: 12.7 mi. N.N.E. Huixtla, 1500′ (UF 20178. 17); 14.6 mi. N.N.E. Huixtla; 2100′ (UF 20179. 2); near Escuintla (UMMZ 128945. 3). Specimens for anatomical studies were taken from the series comprising UF 20178.

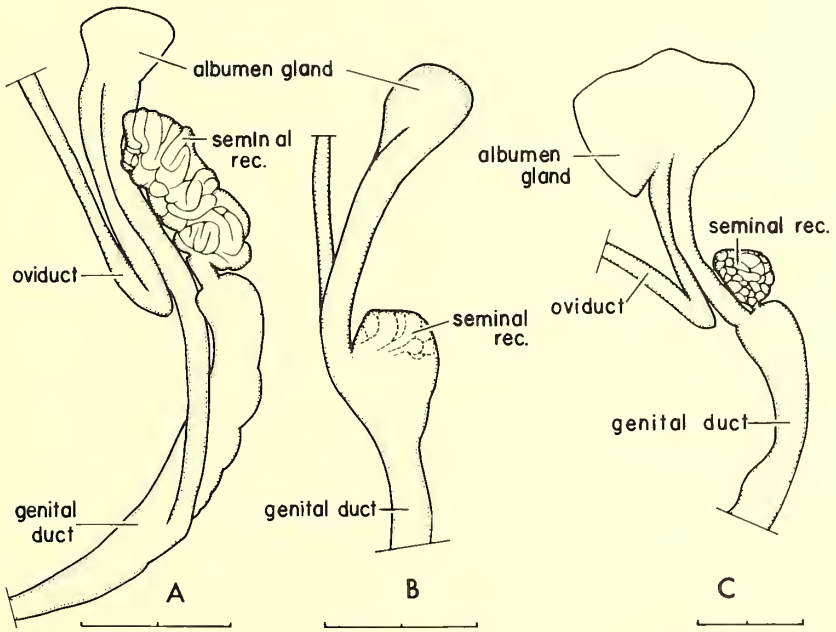
This subspecies was common north of Huixtla in quasi-rain forests, where specimens were collected in leaf mulch and among organic debris.

Remarks. Solem (1956: 45) treated this form as *A. t. texturatus* (Sowerby), but noted the distinctive characteristics of its color patterns. It is distinguished from *A. texturatus* by its spiral banding. It also tends to be more elevated and to have a narrower umbilicus, but it overlaps the typical subspecies in these characters.

Amphicyclotus paulsonorum new species

Diagnosis. A species of the typical subgenus characterized by its small size, large umbilicus, costulate sculpture on the second embryonic whorl, and loosely convoluted seminal receptacle.

Shell (Pl. VI, D-F). Moderately small. Solid, but not thick-walled. Periostracum uniform dull yellow-brown. Depressed-helicoid in



Text-fig. 10. Posterior view of terminal segments of the genital ducts and associated structures in three species of *Amphicyclotus*. A. *A. paulsonorum* new species, topotype. B. *A. parvus* Thompson, paratype. C. *A. t. spiralis* new subspecies, topotype. Scales equal 2 mm.

Measurements in mm of six large specimens from the type series of *A. paulsonorum* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
20.5	15.0	13.5	5.0	9.2	9.2	holotype
20.5	15.5	13.7	5.4	8.9	9.0	paratype
20.1	14.8	13.0	5.2	8.7	8.7	paratype
20.0	14.6	13.1	4.8	9.5	9.2	paratype
19.4	14.2	12.7	4.6	8.8	9.0	paratype
19.0	14.6	11.7	5.0	8.3	8.2	paratype

shape; height 0.62-0.69 times major diameter. Spire broadly conical, pointed; spire nearly straight-sided. Umbilicus moderately wide, deep and funicular, 0.23-0.27 times major diameter. Whorls slowly and regularly increasing in size; minor diameter 0.72-0.77 times major diameter. Whorls flattened dorsally along the suture and tending to be obsoletely angulate along the periphery. Last whorl not descending near the aperture. Suture deeply impressed, but not channeled. Whorls 4.6-5.0 (4.9 in holotype). Embryonic whorls, 2.0; *moderately protruding and with a strongly impressed suture.* First embryonic whorl smooth; following whorl with strong, close, moderately oblique ribs. Following neanic whorl with stronger, more widely spaced, and nearly vertical ribs that become wavy near the suture. Remaining whorls with moderately strong, vermiculated sculpture that forms oblique wavy lines along the periphery and is continuous into the umbilicus. Sculpture tending to be obsolete along the last ¼ whorl, particularly on the base. Aperture circular, oblique in lateral profile; interior white. Aperture width 0.43-0.46 times major diameter. Peristome simple, narrowly interrupted across parietal margin. Parietal callus moderate and opaque in large individuals.

Operculum. Chitinous, consisting of about eight vaguely distinguishable whorls that do not overlap. Concave, with the nucleus depressed on the outer surface and forming an obtuse blunt point on the inner surface.

Male (Text-fig. 8, E-F). The male reproductive system is similar to that of *A. texturatus*, but differs in several characteristics of the verge. The distal third of the verge is broadly expanded so that the recurved penis is of minor importance in its mass. The funicular tip of the penis lies along the inner margin facing the base of the verge, and the penial bulge is large and lobate.

Female (Text-fig. 9, A). The nature of the uterus and vagina is similar to that described for *A. texturatus* and the genus in general. Features peculiar to *paulsonorum* are in the structure of the genital duct and its associated organs. The duct is open throughout most of its length and forms a moderately small vestibule at its distal end. The seminal receptacle is large and consists of a highly convoluted mass of tubules that are loosely connected so that no compact structure is formed. (In Text-fig. 9, A, the receptacle is folded upon itself so that its true relative size is not indicated). The receptacle discharges through a small duct into the apex of the vestibule (Text-fig. 10, A). The albumen gland consists of a moderately enlarged sacculate loop in the oviduct, and has a relatively long duct that enters the genital duct about midway between the apex and the vagina.

Type Locality. A ravine 4.2 mi. N. W. Escuintla, Chiapas; 300 feet altitude. Holotype: UF 20180; collected 24 July, 1966 by Fred G. Thompson. Paratypes: UF 20181 (15), UMMZ 216549 (5); same data as the holotype.

Other Specimens Examined. Chiapas: 21.3 mi. N. W. Huixtla, 300′ (UF 20182. 17); 32.5 mi. N. W. Huixtla, 200′ (UF 20184. 2); 10 mi. N. W. Pijijiapan, 100′ (UF 20183. 6). Alcoholic specimens for anatomical studies were taken from the type series and the two localities northwest of Huixtla.

This species was collected in quasi-rain forests. They were found crawling on debris and leaf mulch after rains, and hiding in organic trash during dryer weather.

Remarks. *A. paulsonorum* is similar to *A. texturatus spiralis* in superficial appearance, but differs in several aspects of the shell, including its smaller size, fewer whorls, unicolor spire, and lack of spiral bands. As far as is known the two species are allopatric. They were suspected to be subspecifically related until their soft anatomies were examined. *A. paulsonorum* differs strikingly from *spiralis* by its larger, loosely coiled seminal receptacle, and by the origin of the oviduct from the middle of the common genital duct (Text-fig. 10, A, C). In *spiralis* the receptacle is smaller and compactly coiled, and the oviduct discharges into the apex of the common genital duct behind the vestibule.

The shell of *paulsonorum* is also similar to that of *A. parvus* Thompson (1963: 20-22) and *A. maleri* Crosse and Fischer (1883: 102). *A. parvus* differs most notably in characteristics of the sculpture. In that species the first 2½ whorls are devoid of any sculpture, except for very fine, irregular growth striations. The following whorls have the characteristic vermiculate sculpturing as occurs in the genus, but the sculpturing is very weak and shiny. *A. paulsonorum* has strong oblique axial ribs on the second embryonic whorl and the following whorl, and the vermiculated sculpture on the remainder of the shell is strong, rugose, and dull. *A. parvus* differs by even more striking characteristics of the female reproductive system. The copulatory bursa is vestigial and is imbedded in the vestibular wall of the common genital duct, and the oviduct originates from the apex of the common duct (Text-fig. 10, B).

A. maleri, from Tabasco, differs from *paulsonorum* by being considerably larger, by having a reddish-violet apex, and by having the uppermost 2.5 whorls smooth.

The specific epithet of *A. paulsonorum* is proposed as an expression of gratitude to Dr. Dennis R. Paulson and his wife Mary Lynn, who discovered the species.

Amphicyclotus parvus Thompson

Amphicyclotus parvus Thompson, 1963; Proc. Biol. Soc. Wash., 76: 20-22; pl: II, figs. 4-7.

Type Locality. Hacienda Monte Cristo, Metapan, Santa Ana, El Salvador; 2200 meters elevation. Holotype: UMMZ 195882. Paratypes: UMMZ 195881 (35); Senckenbergischen Naturforschenden Gesellschaft 101151-6 (120).

No new material has been examined. The following anatomical discussions are based upon animals extracted from the paratypes (UMMZ 195881), which were preserved in 70% alcohol when collected.

Male (Text-fig. 8, A-B). The male reproductive system is similar to that of *A. texturatus.* It differs only by having a smaller "penial" bulge along the right margin, and by having a more pronounced funicular tip to the verge.

Female (Text-fig. 9, C). The female reproductive system is similar to that of *A. texturatus* except for the following characters. The distal end of the genital duct forms a much enlarged vestibule. The seminal receptacle is rudimentary, being embedded within the wall of the vestibule and is evident only as convoluted tubules within the wall. The albumen gland is relatively smaller, as is illustrated.

Amphicyclotus megaplanus Morrison

Amphicyclotus megaplanus Morrison, 1955; Jour. Wash. Acad. Sci., 45: 160; figs. 29-31.

Morrison's description is based upon a bleached and worn adult (holotype) and an immature paratype. The holotype (USNM 618777) lacks the apical whorls, the operculum, and the periostracum. The paratype (USNM 618778) has worn apical whorls and lacks an operculum. Material recently collected from near the type locality reveals several important features not evident or clearly represented in the type material, and necessitates a redescription of the species.

Shell. Large, solid, light brown with occasional darker growth streaks. Planular, height 0.54-0.56 times major diameter. Spire broadly conical and slightly elevated; sides of spire concave. Apical whorls protruding. Whorls rapidly increasing in size; minor diameter 0.70-0.78 times major diameter in large specimens. Umbilicus broad and revealing all previous whorls; umbilicus 0.27-0.30 times major diameter. Suture deeply impressed and channeled, particularly along last whorl, which rapidly descends near the aperture. Whorls flattened and sloping inward near the suture; uniformly rounded around the periphery. About 5.3 or more whorls in mature specimens (apex frequently broken or eroded). About 2.0 embryonic whorls, which bare sparse, oblique, weak axial riblets along the upper suture. Riblets continuing on following two postembryonic whorls. Last 1.3 whorls with characteristic but weak vermiculate sculpture that continues over the surface of the whorl and into the umbilicus, but may be obsolete on some parts of the base near the aperture. The vermiculated sculpture may be hardly noticeable in some specimens, particu-

Measurements in mm of five specimens of *A. megaplanus* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
42.0	32.5	22.5	12.6	16.0	18.0	holotype*
37.0	26.9	20.8	10.7	15.0	16.1	
34.9	25.0	19.6	9.6	14.0	15.6	
32.5	27.0	18.0	—	14.0	14.0	paratype*
31.4	22.0	—	9.4	12.9	14.0	

* Measurements given by Morrison (1955: 160).

larly those with fewer than 4.5 whorls. Aperture nearly circular, slightly wider than high; width of aperture 0.43-0.45 times major diameter. Peristome continued across parietal margin by a thick callus. Posterior corner of aperture with a weak, impressed groove and advanced as a small point. Aperture strongly oblique in lateral profile and slightly sinuous. Interior white.

Operculum (Pl. I, I). Nearly planular; slightly depressed in the center and with a low knob over the inner surface of the nucleus. Consisting of about 9 closely coiled whorls. Outer surface with a moderately thick spiral calcareous layer. Chitinous basal plate thin and with oblique weak lamella that are worn away at the outer surface of the operculum. Spiral calcareous lamellum highest along inner margin and sloping outward.

Male (Text-fig. 8, C-D). The verge is similar in location and structure to that of other members of the genus. The distal end forms a large funicular opening in which the seminal groove terminates.

Female. None examined.

Type Locality. Ocozocoautla, Chiapas. Holotype: USNM 618777. Paratype: USNM 618778.

Specimens Examined. Chiapas: 15.8 mi. N. W. Ocozocoautla, 2700 ft. alt. (UF 20174. 3), (UF 19180. 2).

Anatomical Material. One male from UF 20174.

Remarks. This species is closely related to other Chiapas members of the genus *Amphicyclotus* s. s., as is indicated by the structure of the verge, the vermiculate sculpture on the shell, and the closely coiled multi-whorled operculum. It differs from all other members of *Amphicyclotus* s. s., as well as the problematic genera *Barbacyclus* and *Megacyclotus* by the presence of a moderately heavy spiral calcareous deposit on the outer surface of the operculum, much as occurs in *Neocyclotus*. On the basis of this character, *megaplanus* could be accorded separate generic status from *Amphicyclotus* as has frequently been done with other members of the family by using such criteria. Because it is closely related to other members of *Amphicyclotus* s. s. by the structure of its verge, and since we know nothing of its female reproductive system, I hesitate to separate *megaplanus* from *Amphicyclotus* s. s. A recent suggestion (Solem, 1956: 46) that *megaplanus* may be subspecifically related to *A. texturatus* (Sowerby) is without basis, and is highly unlikely because of the opercular differences.

Barbacyclus Bartsch and Morrison

Barbacyclus Bartsch and Morrison, 1942; Bull. U. S. Nat. Mus., 181: 175. (Type species: *Cyclophorus underwoodi* Da Costa, 1900).

Bartsch and Morrison separated *Barbacyclus* from *Amphicyclotus* and allied genera by the forward projection of its upper lip, its spiral banding, its strong oblique thread-like sculpture, and its operculum which bears fimbriations along the outer edge of each turn. Solem (1956: 43) expressed doubt about the generic significance of these characters. Material pertaining to this genus is still rare in collections, and the only information on its anatomy is provided in the short description given below for *B. princeps* (Pilsbry). The anatomical material that I have examined is limited to a single incomplete male, but indicates that *Barbacyclus* is distinct from *Amphicyclotus* by the possession of a small spoon-like penis at the tip of the verge. Because of this anatomical distinction, I tentatively favor the recognition of *Barbacyclus* as generically distinct from *Amphicyclotus,* though the two are close in their relationship.

Barbacyclus princeps (Pilsbry)

Aperostoma (*Amphicyclotus*) *princeps* Pilsbry, 1935; Proc. Acad. Nat. Sci. Phila., 87: 3; pl. 1, figs. 1, 1a, 1b.

Barbacyclus princeps (Pilsbry), Bartsch and Morrison, 1942; Bull. U. S. Nat. Mus., 181: 175-176; pl. 23, figs. 1-3.

Costa Rica (Limon Prov.): Moin Hill, nr. Limon (UF 20143. 20), (UF 20144. 20), (UF 20145. 3), (UF 20147. 2), (UF 20146. 1); all lots collected by Colin Little.

The material is rather homogeneous in character, and its variation is not sufficient to include other named forms. One single shell contained a partially decomposed animal that was in sufficient condition to provide the following notes on its reproductive anatomy.

Male (Text-fig. 7, D-E). The verge is located on the center of the nape beneath the mantle collar, and is directed posteriorly when relaxed. The verge is nearly uniform in diameter throughout its length, and is terminated by a thin, fleshy, spoon-like penis. An open seminal groove extends from the anterior end of the prostate across the nape and along the ventral surface of the verge to the penis. The seminal groove is bounded on either side by large ridge-like folds that continue to the tip of the verge.

Neocyclotus Fischer and Crosse, 1886

As used in this paper, *Neocyclotus* includes as subgenera *Neocyclotus s. s., Incidostoma*

Bartsch and Morrison, 1942 (see Morrison, 1955: 157), and *Cyclohidalgoa* Bartsch, 1942. This last group lies beyond the geographic limits of this paper, and anatomical material pertaining to it is not available.

Neocyclotus is a large genus distributed through most of tropical South America, the Lesser Antilles, and Central America north to Veracruz, Mexico. The genus is represented in Mexico and Central America by a few species of two subgenera, *Neocyclotus s. s.* and *Incidostoma*. Our knowledge of the anatomy of the genus consists of a description of the female reproductive system of *N. dysoni* (Pfeiffer) (Tielecke, 1940: 338-339), some brief observations on the external male reproductive structures of *N. wetmori* (Bartsch and Morrison), *N. grenadensis mcsweeni* (Bartsch), *N.* (*I.*) *giganteum* (Reeve), and *N.* (*C.*) *translucidum bejumense* (Baker) (Morrison, 1955: 156-157), and the anatomical observations given below representing the type of the genus (*N. dysoni*), some closely related species, and a single species of the subgenus *Incidostoma*.

Neocyclotus is characterized anatomically by having an elongate dorso-ventrally compressed verge that is terminated by a simple flagellum-like penis lying along the ventral distal margin and between two labiate folds of flesh (Text-fig. 11, D-F). A seminal groove extends from the anterior end of the prostate, across the nape, and along the ventral side of the verge to the tip of the penis. The seminal groove may be open (*Incidostoma*), or it may be secondarily coalesced by a raphe to form an internal sperm duct and a superficial seminal furrow overlying the duct (*Neocyclotus*). The prostate is simple in structure, with a semicircular lumen resulting from a partial involution on the ventral side. The oviduct forms a sigmoid loop at the distal end of the uterus. The distal segment of the loop is enlarged into an albumen gland. The seminal receptacle is large, globular, hollow, and has a short stout duct that connects to the oviduct. The genital duct enters the wall of the uterus and about halfway above the vagina becomes enlarged and folded as part of the uterus (Text-fig. 13). The uterine lumen is divided by a complete involution of the ventral wall. This forms two chambers that interconnect at the distal end, so that a single long sigmoid passage is formed from the common genital duct to the vagina (Text-fig. 13, B). The vagina is short and is confined to the anterior end of the uterus.

The two subgenera considered do not differ significantly in the female reproductive system. They are readily recognized by conchological features. *Incidostoma* has a bicolor shell with simple costutate sculpture, and a tightly coiled operculum with 8 to 11 whorls. *Neocyclotus* has a unicolor shell that generally has anastomosing sculpture, and the operculum contains about 5 to 6 rapidly expanding whorls. These differences might be considered sufficient basis for separating the two as genera, but the close anatomical similarity between them and the intermediate nature of some species overshadows their distinctiveness. Also we do not know the variability of opercular and anatomical characters among the South American species of *Incidostoma* or *Neocyclotus*.

Neocyclotus s. l. is closely related to a large assemblage of West Indian genera. These include *Cyclopilsbrya* Bartsch, 1942; *Cyclobakeria* Bartsch, 1942; *Cyclojamaicia* Bartsch, 1942; *Cyclochittya* Morrison, 1955; *Poteria* Gray, 1850; *Plectocyclotus* Kobelt and Moellendoriff, 1898; and probably *Rugicyclotus* Morrison, 1955. These genera are closely allied by the terminal structure of the verge (Morrison, 1955). All possess a verge similar to that found in *Neocyclotus*, in contrast to all other neotropical genera which have basically different male reproductive structures. Morrison's observations are not detailed enough to allow an analysis of generic interrelationships, for he only examined the external male genitalia. A large closely related assemblage of genera such as this might be considered worthy of subfamilial recognition, except that in this instance the generic taxonomy is "over refined" and exaggerates the true degree of differentiation.

Besides the species and subspecies listed below, *Neocyclotus* includes several additional Central American and Mexican forms (*see* Bartsch and Morrison, 1942: 204-219, 233-242. Solem, 1956: 53-54).

Subgenus **Neocyclotus** Fischer and Crosse, 1886

Neocyclotus Fischer and Crosse, 1886; Miss. Sci. Mex., 2: 148. – Morrison, 1955; Jour. Wash. Acad. Sci., 45: 156. (Type species: *Cyclostoma dysoni* Pfeiffer, 1851).

Austrocyclotus Bartsch, 1942; Bull. U. S. Nat. Mus., 181: 133. (Type species: *Cyclostoma stramineum* Reeve, 1843).

Neocyclotus s. s. is a specialized subgenus evolved from a more generalized South American lineage. This is suggested by both its anatomy and its geographic distribution. The coalesced seminal groove forming a sperm duct in the male is derived from the more generalized condition of an open groove such as occurs in *Incidostoma*. The geographic distribution of *Neocyclotus s. s.* in Central America and Mexico indicates a group that relatively recently has

immigrated northward from South America and has not yet undergone much evolutionary diversity at the specific level. In contrast, several very distinct species of *Neocyclotus s. s.* occur in northern South America and the Lesser Antilles. The migration northward from South America probably was initiated in the early Pliocene when Central and South America became connected. The distribution and differentiation of *N. dysoni* in Mexico suggests an even more recent immigration of the genus into that region.

Neocyclotus dysoni ambiguum (Martens)

Cyclotus (*Aperostoma*) *dysoni ambiguum* Martens, 1890; Biol. Cent. Amer.: 4.

Neocyclotus dysoni ambiguum (Martens), Kobelt and Möllendorff, 1897; Nachrb. Deutsch. Malak. Ges., 29:137. – Solem, 1956; Proc. Acad. Nat. Sci. Phila., 108: 53.

Poteria (*Neocyclotus*) *dysoni ambiguum* (Martens), Baker, 1923; Occ. Pap. Mus. Zool. Univ. Mich., (137): 34.

Aperostoma (*Neocyclotus*) *dysoni ambiguum* (Martens), Bartsch and Morrison, 1942; Proc. U. S. Nat. Mus., 181:211; pl. 28; figs. 10-12.

Veracruz: Laguna Encontado, nr. San Andres Tuxtla (UF 19163, 56). Tabasco: 2.4 mi. E. Teapa (UF 20213. 1); 2.6 mi. E. Teapa (UF 19167. 3); 4.0 mi. W. Teapa (UF 19166. 3). Chiapas: 8.0 mi. N. Tuxtla Gutierrez, 3800′ (UF 19297. 22); 8.6 mi. E. Chiapa de Corzo, 3100′ (UF 19164. 10); 14.9 mi. E. Chiapa de Corzo, 4400′ (UF 19165. 5).

Anatomical Specimens. Chiapas: 8.6 mi. E. Chiapa de Corzo (4 females, 3 males).

Male. The prostate (Text-fig. 11, B-C) is baso-columellar in position and is a simple tapering clavate structure that is enlarged distally and pointed basally. Its surface is finely furrowed due to underlying glandular lobes. The prostatic lumen (Text-fig. 11, C) is a semicircular cavity that is lined on two sides by thick glandular layers. The dorsal layer is derived from a partial involution, but the interior is not divided into two interconnected chambers, as in *Dicrista* and *Amphicyclotus*. The verge (Text-fig. 11, D-F) lies on the center of the nape and is coiled and folded clockwise and posteriorly. The verge is broadly expanded at the base and gradually tapers distally. The tip of the verge bears a cleft that is bordered on its two sides by labiate folds. A slender terminal flagellum originates at the base of the cleft and along one side. Distally it bears a shallow groove along its dorsal side into which the sperm duct terminates. A strong fleshy fold extends across the nape from near the end of the prostate to the base of the verge, and continues along the ventral side of the verge as a shallow seminal furrow. The furrow is highly variable due to the state of relaxation of the verge, and may appear as a deep groove. The sperm duct (Text-fig. 11, E-F) is an enclosed tube that extends from the prostate to the tip of the flagellum at the distal end of the verge. It lies within the nape fold and beneath the seminal furrow. The sperm duct is derived from a deep seminal groove, for it is connected to the outer surface of the nape and verge by a coalesced and keratinized raphe. The overlying nape fold and seminal furrow have been wrongly interpreted as a seminal groove by other authors.

Female (Text-fig. 13, A). The uterus is stocky, short and dorso-ventrally compressed distally. The outer and distal margins have numerous large lobes caused by the pattern of the underlying glandular fold in the uterine wall. The vaginal slit is short and is near the anterior end of the uterus. The interior of the uterus is divided into two chambers by a thick involution that extends to the opposite wall (Text-fig. 13, B-C). The chambers are interconnected distally. The vaginal slit opens into the right chamber, which serves as a functional vagina. The left chamber has a U-shaped loop at its anterior end, which is caused by the side of the uterus being folded back upon itself. The genital duct discharges into the uterine chamber at the end of this folded loop. The oviduct forms an elongate sigmoid loop along the distal end of the uterus. The distal segment of the loop is slightly enlarged and forms a lobate albumen gland. The lower segment of the loop is tightly attached by connective tissue to the ventral side of the uterus. The seminal receptacle is large, globular, hollow; is partially impressed in the ventral side of the uterus; and is attached to the oviduct by a short duct. The two ducts form a genital duct that is imbedded in the uterine wall and enters the uterus one-third of the distance above the vagina.

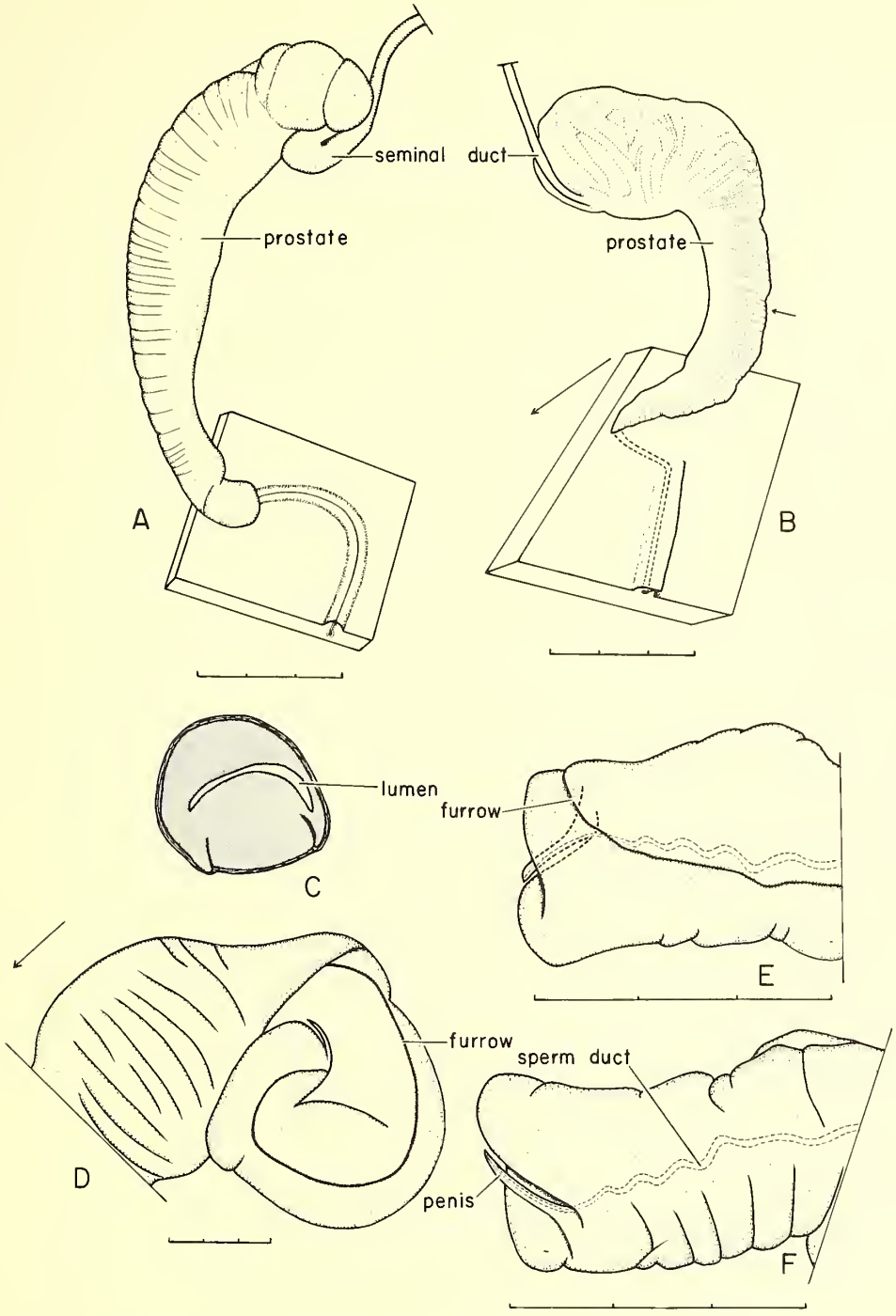
Neocyclotus dysoni dysoni (Pfeiffer)

Cyclostoma dysoni Pfeiffer, 1851; Proc. Zool. Soc. Lond., 19: 243. – Pfeiffer, 1852; *in* Martini-Chemnitz, Conchylien Cabinet, 1, sec. 19: 259; pl. 35, figs. 5-6.

Neocyclotus dysoni (Pfeiffer), Fischer and Crosse, 1888; Miss. Sci. Mex. l'Amer. Cent., 2, (7): 164, *in part.*

Cyclotus (*Aperostoma*) *dysoni* (Pfeiffer), Martens, 1890; Biol. Cent. Amer.: 3.

Aperostoma (*Neocyclotus*) *dysoni dysoni* (Pfeiffer), Bartsch and Morrison, 1942; Proc. U. S. Nat. Mus., 181: 207-208; pl. 28, figs. 28-30.



TEXT-FIG. 11. Male reproductive structures of *Neocyclotus*. A. *N. bisinuatus* (Martens), prostate; Tapanti, Costa Rica. B. *N. d. ambiguum* (Martens), prostate; 8.6 mi. é Chiapa de Corzo, Chiapas. C. Cross-section through prostate of B at point indicated by arrow. D-F. *N. d. ambiguum* (Martens), dorsal view of verge (D) and enlarged illustrations of dorsal (E) and ventral (F) views of the terminal portion of the verge showing the relationships of the sperm duct to the seminal furrow and the penis. Scales equal 3 mm.

Honduras (Comayagua Prov.): 4 Km. S. S. W. (Comayagua, stream drift (UF 20165. 1); 15.1 mi. N. Comayagua, 4200' (UF 19162. 17).

Neocyclotus dysoni dyeri (Bartsch & Morrison)

Aperostoma (*Neocyclotus*) *dysoni dyeri* Bartsch and Morrison, 1942; Proc. U. S. Nat. Mus., 181: 205; pl. 28, figs. 31-33. – Solem, 1956; Proc. Acad. Nat. Sci. Phila., 108: 54. (Type locality: La Ceiba, Honduras).

Honduras (Colon Prov.): Balfate (UF 20166. 5).

This is a giant subspecies confined to the coastal region of northern Honduras and adjacent regions of Guatemala. Specimens from Balfate, Honduras, have a distinct notch in the basal lip, as in specimens discussed by Solem (1956:54). In this respect they tend to approach *N. bisinuatus* (von Martens) from Costa Rica, but I have not examined sufficient material from Nicaragua to demonstrate intergradation.

Neocyclotus dysoni nicaraguense
(Bartsch and Morrison)

Aperostoma (*Neocyclotus*) *dysoni nicaraguense* Bartsch and Morrison, 1942; Proc. U. S. Nat. Mus., 181: 214-215; pl. 29, figs. 16-18.

Costa Rica (Guanacaste Prov.): 3.8 mi. S. Nicoya (UF 20162. 9); 2.2 mi. S.E. Nicoya, 500' (UF 20163. 50); 1.2 miles east of Caimital (UF 20164. 26).

This subspecies was described from the dry Pacific coastal region of Polvón, Nicaragua. Its occurrence in Costa Rica is an extension of its known range southward to the Nicoya Peninsula.

Neocyclotus simplicostus new species

Diagnosis. A species of the subgenus *Neocyclotus* distinguished from all others by having simple costulate sculpture. It is closely related to *N. dysoni* (Pfeiffer) by its opercular structure and its anatomy, but is distinguished by its smaller size as well as its sculptural characters.

Description (Pl. II, J-L). Shell small, light brown, becoming slightly lighter on base and in umbilicus. Dull satiny. Helicoid, height 0.74-0.83 times major diameter. Spire elevated, conical; nearly straight sided, being very slightly convex. Whorls rapidly increasing in size; minor diameter 0.69-0.84 times major diameter. Umbilicus moderately sized, but highly variable, about 1/5-1/10 of major diameter. 4.0-4.4 whorls in mature shells (4.3 in holotype). Suture strongly impressed. Whorls nearly uniformly rounded; slightly extended peripherally; weakly shouldered. Last whorl usually not descending near the aperture. Embryonic whorls 1.7-1.9; smooth. Following whorl or so with irregular weak axial striations which become more intense and transform into ribs on last quarter of penultimate whorl. Body whorl with strong parallel, slightly oblique axial ribs that continue only slightly diminished across base and into umbilicus. In contrast with other species of *Neocyclotus* the ribs do not anastomose. Aperture large, broadly ovate, slightly indented along parietal margin; hyaline white internally; slightly oblique in lateral profile. Aperture width 0.49-0.54 times major diameter. Peristome simple, continued across parietal margin by a callus.

Operculum (Pl. I, J). Solid and calcareous. Consisting of about six whorls that rapidly increase in size. Nucleus sunken. Each succeeding whorl lying on a slightly higher plane than previous whorls. Inner edge of whorls forming a slightly raised spiral chord. Chitinous basal plate forming a small knob under nucleus; not extending through outer calcareous surface.

Male (Text-fig. 12, E). The verge is similar to that of *N. d. ambiguum*, except smaller. It ends in a slender flagellar extension that lies between two terminal labia. The sperm duct is enclosed within the verge, but is connected to the seminal furrow by a coalesced raphe. The sperm duct continues internally from the prostate to the tip of the flagellum. There is a low

Measurements in mm of the ten largest specimens from the type series of *N. simplicostus* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
14.8	11.3	12.2	1.4	8.3	8.0	holotype
15.4	12.9	12.2	2.3	8.2	7.6	paratype
15.4	11.9	12.2	2.0	8.1	7.6	paratype
14.9	11.3	11.4	2.6	8.1	7.3	paratype
14.0	10.5	10.6	2.3	7.8	7.1	paratype
14.1	10.2	10.4	2.7	7.7	7.2	paratype
14.7	10.9	11.3	1.7	7.7	7.3	paratype
14.5	10.0	11.5	1.7	7.6	7.1	paratype
13.1	10.0	10.1	1.6	7.2	6.4	paratype
13.7	10.0	10.4	2.0	7.3	7.1	paratype

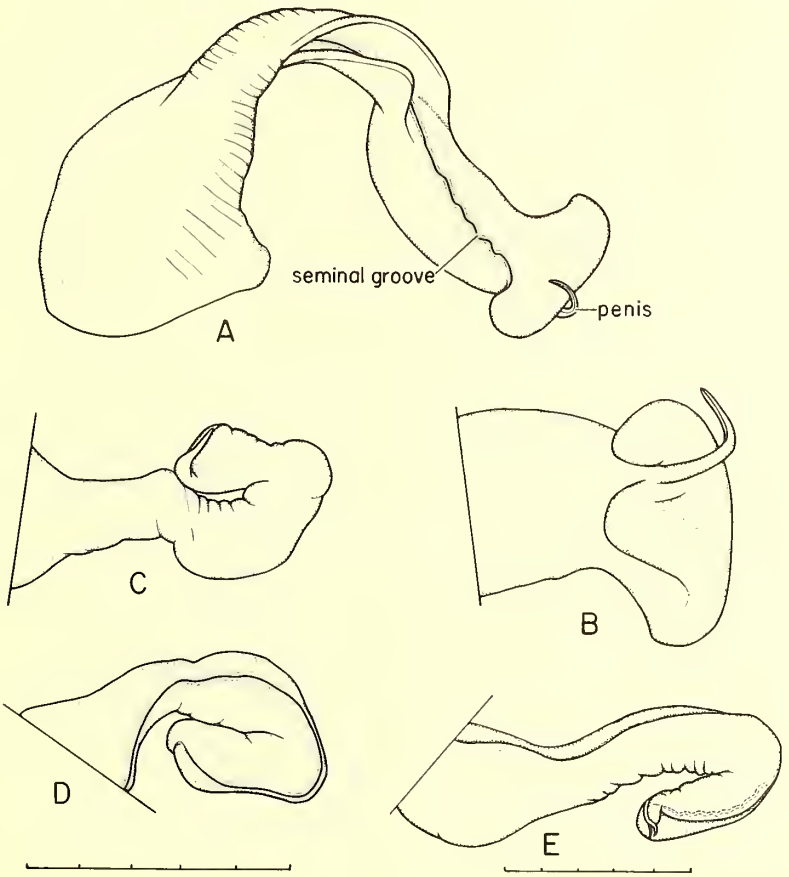
ridge on the nape overlying the sperm duct and extending from the prostate to the base of the verge, where it continues as the seminal furrow.

Female (Text-fig. 13, D). The uterus and associated organs are similar to those of *N. d. ambiguum* though smaller. The seminal receptacle is more elongate, and the lower part of the genital duct converges into the uterus more rapidly.

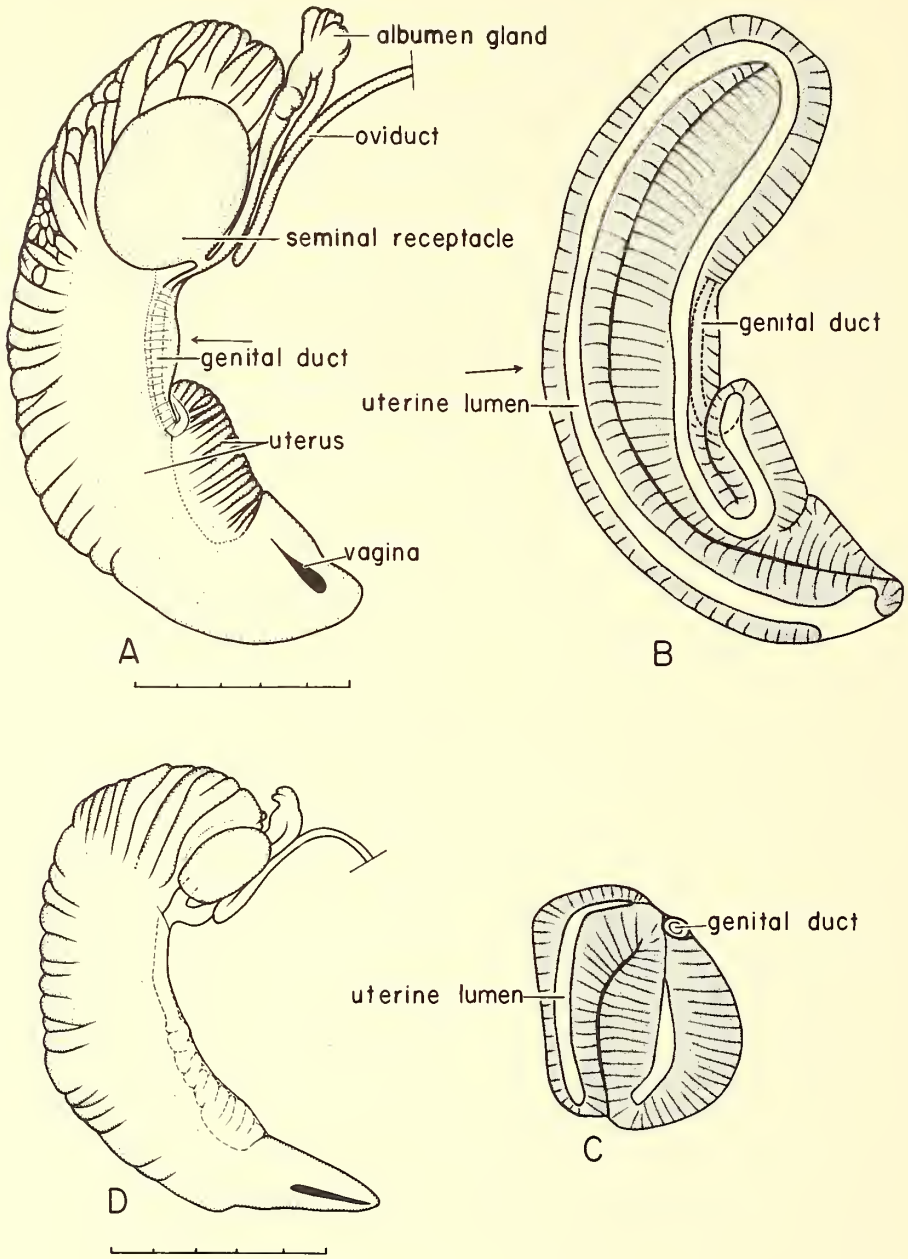
Type Locality. A ravine 4.2 miles northwest of Escuintla, Chiapas; 300 feet altitude. Holotype: UF 20167; collected 24 July, 1966 by Fred G. Thompson. Paratypes: UF 20168 (30), UMMZ 216559 (5); same data as holotype. The type series was collected in leaf mulch and debris in a second growth quasi-rain forest, along the side of a ravine. The soil consisted of lateritic clay.

Other Specimens Examined. UF 20171 (19 spec. in alcohol from type locality). Chiapas: 21.3 mi. N. W. Huixtla, 300′ (UF 20169. 33); 32.5 mi. N. W. Huixtla, 200′ (UF 20170. 3), (UF 20172; 2 spec. in alcohol).

Geographic Variation. This species is known only from the vicinity of Escuintla, Chiapas. It shows considerable variation between the three known populations. Specimens from 21.3 mi. N. W. Huixtla differ from the typical form in that the axial ribs on the base are weaker, and form sharp threads in the umbilicus. The specimens from 32.5 mi. N. W. Huixtla are considerably larger than those of other populations, attaining a major diameter of 19.5-21.1 mm, but are typical in proportions. They also differ in that they have stronger ribs on the base and in the umbilicus. In other aspects of the sculpture they are like the typical form.



Text-fig. 12. Male reproductive organs of three species of *Neocyclotus*. A. *N. bisinuatus* (Martens), dorsal view of verge; Tapantí, Costa Rica. B. *N. bisinuatus* (Martens), enlargement of distal end of verge from ventral view. C-D. *N.* (*Incidostoma*) *impressus* new species, dorsal and ventral views of verge; topotype. E. *N. simplicostus* new species, ventral view of verge; topotype. Scales equal 5 mm; scale on left for A, C, D; scale on right for E only.



TEXT-FIG. 13. Female reproductive systems of two species of *Neocyclotus*. A. *N. d. ambiguum* (Martens); 8.6 mi. é. Chiapa de Corzo, Chiapas. B. Diagramatic longitudinal section through uterus of A showing course of uterine lumen. C. Cross-section of uterus of A at point indicated by arrow. D. *N. simplicostus* new species, topotype. Scales equal 5 mm.

Remarks. *N. simplicostus* differs from all other species of the subgenus by its simple, uniform axial riblets that do not anastomose. It is also distinguished from other species by its smaller size. The distinction of sculpture is more than can be accounted for by assuming that it is only a local variation of the widely distributed *N. dysoni*. A form of the latter species was collected at 14.6 mi. N. N. E. Huixtla, 2100′ (UF 20160). It is typical in its sculpturing and shows no tendency to converge with the characters of *N. simplicostus*.

Neocyclotus bisinuatus (Martens)

Cyclotus bisinuatus Martens, 1864; Malak-Blatter; 11: 113; pl. 3; figs. 1, 2.

Cyclotus (Aperostoma) bisinuatus (Martens), Martens, 1890; Biol. Cent. Amer.: 3.

Neocyclotus (Neocyclotus) bisinuatus (Martens), Kobelt and Mollendorff, 1897; Nachrb. Deutsch. Malak. Gesell., 29: 137.

Aperostoma (Aperostoma) bisinuatus (Martens), Bartsch and Morrison, 1942; Proc. U. S. Nat. Mus., 181: 235; pl. 33, figs. 5-6.

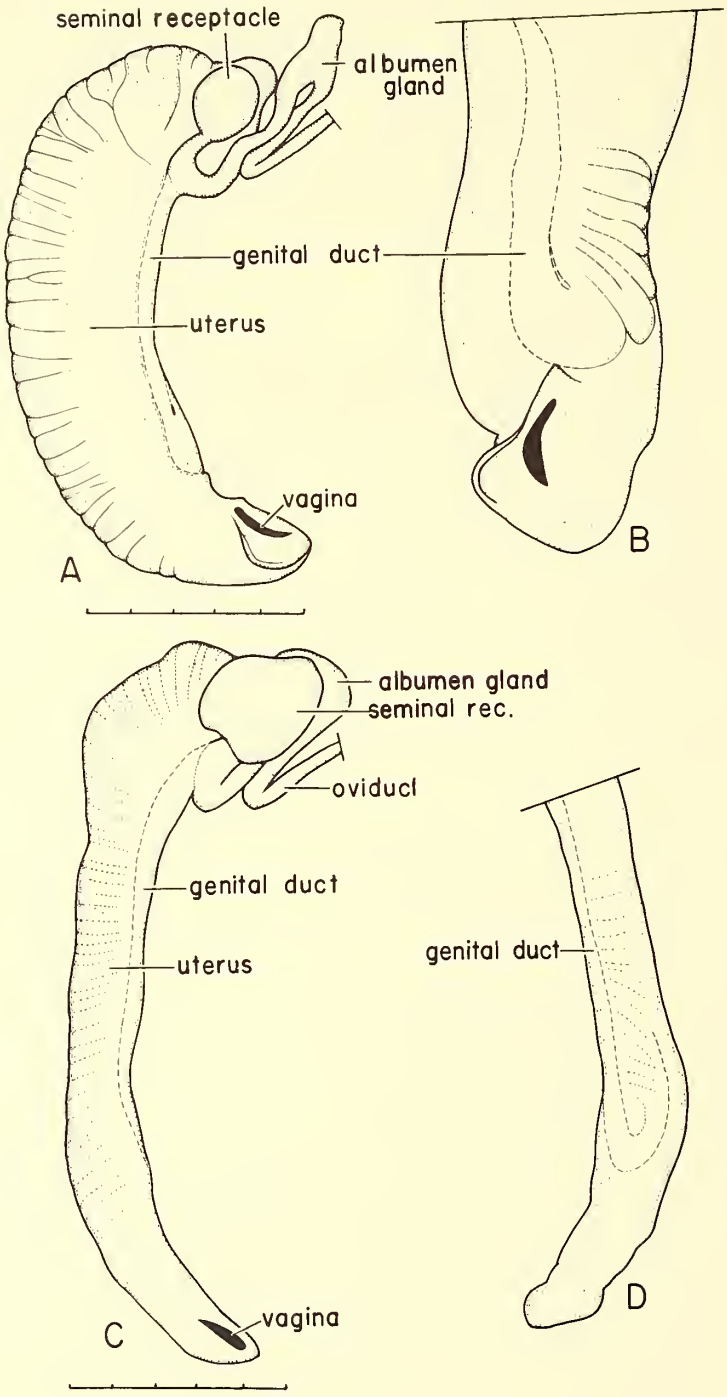
Costa Rica (Cartago Prov.): Tapantí, 4300′ (UF 20159. 13), (UF 20156. 18). (Puntarenas Prov.): 5 mi. E. Villa Neily (UF 20157. 1); Inter-American Agricultural Institute, Turrialba, 2000′ (UF 20158. 1). Anatomical material was examined from each locality.

This species is widely distributed in Costa Rica, and has been recorded from Guatemala (Martens, 1890: 3). Its relationship to *N. dysoni* (Pfr.) is very close, but it is uncertain whether the two species are conspecific. Bartsch and Morrison (1942: 235) placed *bisinuatus* in *Aperostoma (Incidostoma* — see Morrison, 1955: 157), because it has a bicolor base as do other species of that subgenus. Unlike other species of *Incidostoma*, and like most species of *Neocyclotus s.s.*, *bisinuatus* has anastomosing sculpture on the lower whorls. Bartsch and Morrison (1942: 213-214) described *N. dysoni valerioi* from Cervantes, Costa Rica, characterized by having the vermiculated sculpture of *N. dysoni* and by having a bicolor base as occurs in *N. bisinuatus*. If *valerioi* is a subspecies of *N. dysoni*, then the only distinction that remains between *dysoni* and *bisinuatus* is the notches in the peristome for which *bisinuatus* was named. All of the material that I have identified from Costa Rica as *bisinuatus* has the peristomal notches, though to varying degrees due to ontogenetic development of this character. None of the material from Costa Rica that I have identified as *N. d. nicaragueuse* shows any indication of such notches. However, some populations of *N. d. ambiguum*, *N. d. cooki*, *N. d. dyeri*, and an undetermined subspecies of *N. dysoni* from eastern Nicaragua show a tendency for a single notch to develop in the lower peristome. On the basis of its sculpture, opercular structure, and reproductive anatomy, *N. bisinuatus* is more closely related to *N. dysoni* (Pfeiffer) than it is to the bicolor species of *Incidostoma*. Whether *N. dysoni* actually integrates with *N. bisinuatus* in eastern Nicaragua and Costa Rica remains to be determined. It seems unlikely because of the differences in the verges.

Operculum (Pl. I, K). The operculum is typical in structure for the subgenus *Neocyclotus*. In large specimens it consists of 5 to 6 rapidly expanding whorls that overlap along the inner margins, so that a spiral ridge that gently slopes on the outside is formed. The calcareous outer lamella bears numerous moderately strong oblique striations. The inner surface has a raised knob over the nucleus.

Male. (Text-fig. 12, A-B). The prostate lies along the dextroventral margin of the coelom, and is tapered anteriorly. The sperm duct forms an enlarged loop prior to where it enters the prostate. The verge is relatively long and slender, with a broadly expanded base and an enlarged funicular tip. Two lateral flaps lie along the posterior (ventral) side of the verge about halfway from the base. A slender flagellum extends beyond the funicular end of the verge. A seminal groove extends from the anterior end of the prostate, across the nape in a broad curve, and along the posterior (ventral) side of the verge to the tip of the terminal flagellum. The groove connects an enlarged underlying duct with the outside surface, and is not coalesced closed, as in *N. dysoni ambiguum* and *N. simplicostus*. Throughout most of its course, the groove and underlying duct lie within a raised seminal ridge. The verge is located on the center of the nape and is directed posteriorly beneath the mantle when relaxed.

Female (Text-fig. 14, A). The uterus and associated structures are similar to those of *N. dysoni*, though more simplified in certain aspects. The oviduct forms a sigmoid loop at the distal end of the uterus. The albumen gland consists of a weakly enlarged segment in the sigmoid loop. The seminal receptacle is simple, globular, and hollow, and is located on a short stout duct that enters the common genital duct which is embedded in the wall of the uterus. This duct enlarges within the uterine wall, and reverses its direction to pass posteriorly as it enters and transforms into a uterine chamber, as occurs in *D. dysoni*. A major point of distinction between the two species is that the lower



TEXT-FIG. 14. Female reproductive systems of *Neocyclotus*. A. *N. bisinuatus* (Martens); Tapantí, Costa Rica. B. *N. bisinuatus* (Martens), enlarged view of lower part of uterus showing transition of genital duct into uterus. C. *N.* (*Incidostoma*) *impressus* new species, topotype. D. *N.* (*I.*) *impressus;* enlarged view of lower part of uterus showing coarse of genital duct into uterus. Scales equal 5 mm.

segment of the common genital duct is not as strongly convoluted as occurs in *N. dysoni*. Other aspects of the utera are very similar.

Neocyclotus capscelius new species

Diagnosis. A species tentatively assigned to the subgenus *Neocyclotus*. It differs from all other species by its fine axial thread-striations, and by its complex operculum which bears a raised spiral calcareous lamella reinforced laterally by thin oblique lamellar-like buttresses.

Shell (Pl. V, E-H). Medium sized, thin and relatively fragile. Uniform satiny brown with occasional irregular dark streaks occurring along growth threads. Very depressed-helicoid; height 0.62-0.68 times major diameter. Spire low, slightly convex in outline. Umbilicus moderately large, about 0.23-0.25 times major diameter. Whorls, 5.0 in holotypes (which is largest complete specimen). Whorls of moderate caliber, slowly increasing in size; minor diameter 0.75 times major diameter. Suture moderately impressed. Last whorl not descending near aperture. Embryonic whorls protruding, pitted, and eroded so that exact number is not determined. First whorl 0.9 mm in diameter perpendicular to initial suture. Sculpture on lower whorls consisting of fine, irregular thread-striations that parallel lines of growth. Sculpture continuing across base only slightly diminished. Aperture circular, oblique in lateral profile; width of aperture 0.45-0.47 times major diameter; interior with a thin livid gloss. Aperture slightly indented by preceding whorl; slightly auriculate due to forward extension of posterior corner. Peristome simple, sharp, continued across parietal margin by a thin callus.

Operculum (Pl. V, H). Consisting of about eight closely coiled whorls. Along its inner margin calcareous lamella abruptly rising above preceding whorls forming a low spiral wall. Numerous thin lamella-like buttresses extend obliquely outward from the spiral ridge. Nuclear region depressed.

Type Locality. A wooded ravine on Cerro de la Muerte, 10.5 kilometers north of San Isidro El General, San Jose Prov., Costa Rica, 5200 feet altitude. Holotype: UF 20148; collected 14 July, 1963 by Richard C. Casebeer. Paratypes: UF 20149 (4); 14.2 km. north of San Isidro El General, 5600 feet.; collected 5 August, 1963 by Fred G. Thompson. Specimens were found at both localities among debris and mosses in densely wooded ravines in the transitional zone between rain forest and cloud forests.

Remarks. In some aspects *N. capscelius* has a youthful appearance, though the holotype probably represents the definitive form of its species. The entity is characterized by its fine thread-striae, low spire, and peculiar operculum bearing a raised calcareous lamella reinforced on the outside by oblique thin lamellar-like buttresses. Its phylogenetic relationships are difficult to determine. By the combination of its characters it has no close relationship to any known species. On the basis of shell features it would be placed in the genus *Dicrista*. Its operculum, which I consider more significant, suggests a relationship with *Neocyclotus*. Within *Neocyclotus* it cannot be clearly assigned to any subgenus, for its characters can be derived from any of three subgenera, *Neocyclotus s. s.*, *Incidostoma* and *Cyclohidalgoa*. The only subgenus within this assemblage that has a tendency for the operculum to vary in the direction exhibited by *capscelius* is *Neocyclotus*. In contrast with other species of *Neocyclotus s. s.*, *capscelius* has a closely coiled operculum as occurs in Central American species of *Incidostoma*. However, all Central American species of *Incidostoma* are bicolored and have heavier sculpture as is described below for *N. (I.) impressus* n. sp. The shell sculpture of *capscelius* tends to be similar to that of *Cyclohidalgoa*, but its operculum differs from that subgenus as it does from *Neocyclotus*. Because of its distinctive features *capscelius* could be placed in a separate subgenus, but this should not be done until its anatomy has been examined so that its relationships can be determined with certainty.

N. capscelius is named for Richard C. Casebeer, who brought this interesting species to my attention.

Subgenus **Incidostoma** Bartsch and Morrison

Incidostoma Bartsch and Morrison, 1942; Bull. U. S. Nat. Mus., 181: 187. — Morrison, 1955;

Measurements in mm of the three largest specimens of *N. capscelius* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
25.6	19.1	15.9	6.3	11.8	11.5	holotype
25.5	19.0	—	6.2	11.6	12.0	paratype
21.4	16.1	14.6	5.0	10.0	10.0	paratype

Jour. Wash. Acad. Sci., 45: 157. (Type species: *Incidostoma malleatum* Bartsch and Morrison, 1942).

Pseudaperostoma Baker, 1943; Naut., 56:135. (Type species: *Cyclostoma inca* (Orbigny, 1835).

This subgenus contains two distinct sections that perhaps should be recognized as subgenera. The typical section possesses a strong siphonal notch in the aperture and occurs in Colombia, Ecuador, Peru, and perhaps Brazil. The other section (*Pseudaperostoma*) lacks a notch, is more widely distributed in South America, and occurs as far north as Costa Rica. Morrison (1955: 157) synonymized the two because a series of one species (*Incidostoma incomptum*) includes individuals that bridge this distinction through ontogenetic development. If one fails to recognize generic characters that develop only after maturity, many genera of mollusks would have to be relegated to synonymy. Such a criterion is highly undesirable, for it would result in a few "megagenera" in those instances where the generic characters are not apparent until the shell has completely developed or the animal has undergone sexual maturity. I follow Morrison's usage of *Incidostoma* rather than propose another name change, only because so many South American cyclophorids are poorly founded and are anatomically unknown.

The Central American *Incidostoma* are divided into two species groups (Bartsch and Morrison, 1942: 233-250). The *carmioli* group is confined to Costa Rica, has fine axial ribs in the umbilicus, and has one or two notches in the peristome. The *giganteum* group occurs in Panama, Colombia, and Ecuador; has heavy axial ribs in the umbilicus; and has a slight angle in the posterior corner of the aperture. Several species in both groups are founded on scant material. A large number are not known from a specific locality, but only a country. The species treated below belong to the *carmioli* group and are from Costa Rica. The material, though limited, adds substantially to our knowledge of this group.

Neocyclotus (Incidostoma) carmioli
(Bartsch and Morrison)

Aperostoma (Aperostoma) carmioli Bartsch and Morrison, 1942; Proc. U. S. Nat. Mus., 181: 233; pl. 32, figs. 19-21.

Costa Rica (Cartago Prov.): Rio Chitaria, 2 km. N. E. Jabillas, 3000'; collected by Andrew Starrett, 3 August, 1957 (UMMZ 216557. 2).

Previously this species was not known from any specific locality, and was represented only by the holotype (USNM 25034) and a single immature paratype (USNM 405227). The specimens collected by Starrett are similar to the holotype in all respects, except that they are a bit larger and have a proportionally higher aperture.

Neocyclotus (Incidostoma) irregulare (Pfeiffer)

Cyclostoma (Cyclotus) irregulare Pfeiffer, 1855; Proc. Zool. Soc. Lond., 23: 117.

Cyclotus irregulare (Pfeiffer), Pfeiffer, 1858; Monogr. Pneumon. Viv., 2: 15. — Reeve, 1864; Conchol. Iconica, 14: pl. 4, fig. 18.

Aperstoma (Aperstoma) irregulare (Pfeiffer), Bartsch and Morrison, 1942; Bull. U. S. Nat. Mus., 181: 236; pl. 33, fig. 4.

Costa Rica (Limon Prov.): Pandora (UF 20150. 1).

This species previously was known from "Costa Rica," but without specific locality. The single specimen examined (Pl. VII, D-F) closely fits Pfeiffer's description and Reeve's figure, differing only in minor details. Pfeiffer's measurements are in error, in part, for they imply a very depressed shell. He gives the dimensions as: major diameter 37 mm; minor diameter 30 mm; height 19 mm. Reeve's figure of the type shows a specimen that is about 26 mm in height. Measurements in mm for the specimen from Pandora are: major diameter, 31.1; minor diameter, 23.9; height, 25.2; aperture height, 15.7; aperture width, 14.7; umbilicus, 5.2; 5.0 whorls. The circumbilical angle is not as strongly developed as in Pfeiffer's specimen, for it is rather weakly indicated.

The operculum consists of about 11 closely coiled whorls (Pl. VII, D). The inner margin of the calcareous lamella is raised and overhangs the preceding whorl. The outer slope is rather coarsely and irregularly sculptured with oblique striations.

Measurements in mm for specimens of *N. (I.) carmioli* are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	*Whorls*
44.0	30.5	30.0	8.5	21.4	20.3	5.0
42.1	30.5	27.7	7.8	21.7	20.0	5.0

Neocyclotus (Incidostoma) impressus
new species

DIAGNOSIS. A member of the subgenus *Incidostoma* belonging to the *carmioli* species group, characterized by small size, wide umbilicus, single notch in the lower peristome, and an impressed dent on the inside of the aperture lateral to the notch. It is similar to *N. (I.) pittieri* (Martens), but differs by being more elevated in spire, and smaller. It is not known whether *pittieri* has the impressed dent that characterizes *impressus*.

SHELL (Pl. VII, A-C, G). Medium sized. Solid, but of variable thickness. Bicolor. The dorsal surface consists of a light tan zone that may have a reddish tinge in its middle, and is bound at the periphery by a reddish brown band. The band blends into the lighter colored base, which is similar in hue to the dorsal surface. The intensity of the color pattern is highly variable, and in most specimens tends to be lighter than in the holotype. Shell depressed helicoid, height 0.62-0.73 times major diameter. Spire low, weakly convex in outline. Umbilicus moderately large, 0.18-0.25 times major diameter. Whorls 4.5-4.8 in mature specimens (4.7 in holotype), of moderate caliber; minor diameter 0.71-0.75 times major diameter. Body whorl descending slightly near aperture. Suture moderately impressed. Embryonic whorls 1.7; moderately protruding; smooth. Following whorls crossed by slightly oblique parallel axial threads that transform into riblets on lower whorls. Riblets on last whorl uniform, diminishing slightly on ventral surface, and coalescing in umbilicus to form sharp thread-riblets. Aperture circular, becoming auriculate at posterior corner, which is advanced along suture; 0.44-0.50 times major diameter. Aperture weakly indented by preceding whorl; livid white internally; lying at an oblique angle. Peristome simple, sharp, continued across parietal margin by a moderately thick callus. Basal lip with a small notch. Midway between the notch and the periphery, the interior of the peristome bears a small impressed dent that occupies the same position as the outer peristomal notch in *N. (I.) exiguum* (Bartsch and Morrison).

OPERCULUM (Pl. I, L). Consisting of about eight closely coiled whorls that uniformly increase in size. Inner margin of calcareous lamella abruptly raised, and gradually sloping outward so that a spiral ridge is formed. Outer slope irregularly sculptured with oblique striations. Nuclear region dished out. Inner surface smooth; with a low conical mound over nucleus.

The anatomical material is not in optimal condition for dissection, but is sufficient to reveal essential aspects of the male and female reproductive system. These systems appear as though the individuals are not in breeding condition. The verge and the structures associated with the genital ducts appear to be normal in development, but the prostate and uterus are slightly atrophied. However, these organs are well enough developed to indicate the species phylogenetic alliances.

MALE (Text-fig. 12, C-D). The verge lies on the center of the nape beneath the mantle collar, and is directed posteriorly when retracted. A deep seminal groove extends from the anterior end of the prostate, across the nape, and the length of the verge along its posterior (ventral) surface. The end of the verge bears two folds which form a funicular tip. A slender terminal flagellum lies at the base of these folds. The seminal groove extends to the tip of the flagellum.

FEMALE (Text-fig. 14, C-D). The female reproductive system is similar to that of *N. bisinuatus* (Martens) but is more simplified. The oviduct forms a stout sigmoid loop. An albumen gland is formed at the distal end of the loop. The seminal receptacle is enlarged, sacculate, and has a short thick duct that connects it to the common genital duct. The latter is imbedded in the wall of the uterus, forms a loop at about 1/5 of the distance above the vagina, and transforms into a segment of the uterus with poorly differentiated folds. The internal course of the uterus is similar to that of *N. dysoni*.

TYPE LOCALITY. Along road immediately east of Nueva Castle, Limón Prov., Costa Rica. HOLOTYPE: UF 20151; collected 30 August, 1967 by Colin Little. PARATYPES: UF 20152

Measurements in mm of five specimens of *N. (I.) impressus* from the type series are:

Maj. Diam.	*Min. Diam.*	*Height*	*Umbil.*	*Aper. H.*	*Aper. W.*	
27.3	20.2	19.7	5.0	13.0	13.1	holotype
28.3	20.6	17.6	7.0	12.8	13.0	paratype
25.9	19.5	17.2	6.3	11.8	11.5	paratype
22.6	16.2	15.8	4.3	10.5	11.0	paratype
21.1	15.1	13.8	4.2	10.0	10.1	paratype

(57), UMMZ 216560 (5); same data as the holotype. The specimens were collected in mulch from between the buttress roots of a large *Ficus* tree.

Other Specimen Examined. Costa Rica (Limon Prov.): Pandora (UF 20153. 2).

Remarks. This species is highly variable in appearance and proportions. The color is variable to the extent that in some specimens the peripheral dark zone is almost indistinguishable. The apertural characters that distinguish it from other known species are developed only after maturity. Thirteen specimens in the type series have matured sufficiently to show the notch and the internal impressed dent in the lower lip. The shell under the dent is thin and fragile, and it may break away so that upon superficial examination a second notch may appear to be present.

This species is similar to *N.* (*I.*) *exiguum* (Bartsch and Morrison) in size and appearance. It is distinguished from the latter species by having a wider umbilicus and a single notch in the peristome, as opposed to having two well developed notches. I am uncertain about its relationship to *N.* (*I.*) *pittieri* (Martens). The last species was described as a variety of *N.* (*I.*) *irregulare* (Pfeiffer). It was only briefly contrasted with *irregulare* and has not been figured. *N.* (*I.*) *pittieri* is more depressed than is *impressus*, and it is larger in size. Martens (1900: 597) states that the type is 29 mm in diameter, 16.5 mm in height and has an aperture 10 mm high. It was described from Salinas Bay, northwestern Costa Rica. Whether or not *impressus* and *pittieri* are conspecific has yet to be demonstrated. Their relationship is close.

References

Angas, G. F.
1879. On the terrestrial mollusca collected in Costa Rica by the late Dr. W. M. Gabb, with descriptions of new species. Proc. Zool. Soc. Lond., 1879: 475-486; pl. 40.

Bartsch, P.
1942. The cyclophorid mollusks of the West Indies, exclusive of Cuba. Bull. U. S. Nat. Mus., 181: 43-143; pls. 9-18.

Bartsch, P., and J. P. E. Morrison
1942. The cyclophorid mollusks of the mainland of America. Bull. U. S. Nat. Mus., 181: 142-278; pls. 19-42.

Clench, Wm. J.
1949. Cyclophoridae and Pupinidae of Caroline, Fijian and Samoan Islands. Bull. Bernice P. Bishop Museum, (196): 1-52.

Fischer, P., and H. Crosse
1870-1902. Mission scientifique au Mexique et dans l'Amerique Centrale. Etudes sur les mollusques terrestres et fluviatiles de Mexique et du Guatemala. 2 volumes.

Kobelt, W.
1902. Cyclophoridae. Das Tierreich, 16: i-xxxix, 1-662.

Martens, E. von
1890-1901. Biologia Centrali-Americana. Mollusca. i-xxviii, 1-702; pls. 1-44.

Morrison, J. P. E.
1955. Notes on American cyclophorid land snails, with two new names, eight new species, three new genera and the Family Amphicyclotidae separated on animal characters. Jour. Wash. Acad. Sci., 45: 149-162.

Pfeiffer, L.
1851. Descriptions of forty-three new species of Cyclostomacea, from the collection of Hugh Cuming, Esq. Proc. Zool. Soc. Lond., 1851: 242-251.
1855. Description of thirty-eight new species of land shells, from the collection of Hugh Cuming, Esq. Proc. Zool. Soc. Lond., 23: 111-119.
1865. Monographia Pneumonopomorum Viventium, III: 1-284.

Solem, A.
1956. The helicoid cyclophorid mollusks of Mexico. Proc. Acad. Nat. Sci. Phila., 108: 41-59; pls. 5-6.

Thiele, J.
1929. Hundbuch Systematischen Weichtierkunde, 1 (1): 1-376.

Thompson, F. G.
1963a. Systematic notes on the land snails of the genus *Tomocyclus* (Cyclophoridae). Breviora, (181): 1-11.
1963b. New land snails from El Salvador. Proc. Biol. Soc. Wash., 79: 19-32.
1967. A new cyclophorid land snail from the West Indies (Prosobranchia), and the discussion of a new subfamily. Proc. Biol. Soc. Wash., 80: 13-18.
1968. *Ceochasma*, A remarkable new land snail from Colima, Mexico. (Gastropoda, Prosobranchia, Helicinidae). Proc. Biol. Soc. Wash., 81: 45-52; figs. 1-21.

Tielecke, H.
1940. Anatomie, Phylogenie and Tiergeographie der Cyclophoriden. Archiv für Naturgeschichte, N. F., 9: 311-359.

Torre, C. de la, and P. Bartsch
1942. The cyclophorid mollusks of Cuba. Bull. U. S. Nat. Mus., 181: 3-42; pls. 1-8.

EXPLANATION OF THE PLATES

Plate I

Opercula of Neocyclotinae.

A. *Xenocyclus patulus* new species, holotype.
B. *Dicrista cooperi* (Tryon), (UF 20190).
C. *Dicrista damianensis* (Solem), holotype.
D. *Dicrista liobasis* new species, holotype.
E. *Dicrista flavescens* new species, holotype.
F. *Dicrista indentata* new species, holotype.
G. *Dicrista petersi* (Solem), holotype.
H. *Dicrista rugosa* new species, holotype.
I. *Amphicyclotus megaplanus* Morrison, (UF 20147).
J. *Neocyclotus simplicostus* new species, holotype.
K. *Neocyclotus bisinuatus* (Martens), (UF 20156).
L. *Neocyclotus (Incidostoma) impressus* new species, paratype.

Plate II

A-C. *Dicrista cooperi* (Tryon), (UF 20190).
D-F. *Dicrista indentatus* new species, holotype.
G-I. *Dicrista flavescens* new species, holotype.
J-L. *Neocyclotus simplicostus* new species, holotype.

Plate III

A-C. *Dicrista liobasis* new species, holotype.
D-F. *Dicrista damianensis* (Solem), holotype.

Plate IV

A-D. *Dicrista petersi* (Solem), holotype.
E-G. *Dicrista rugosa* new species, holotype.

Plate V

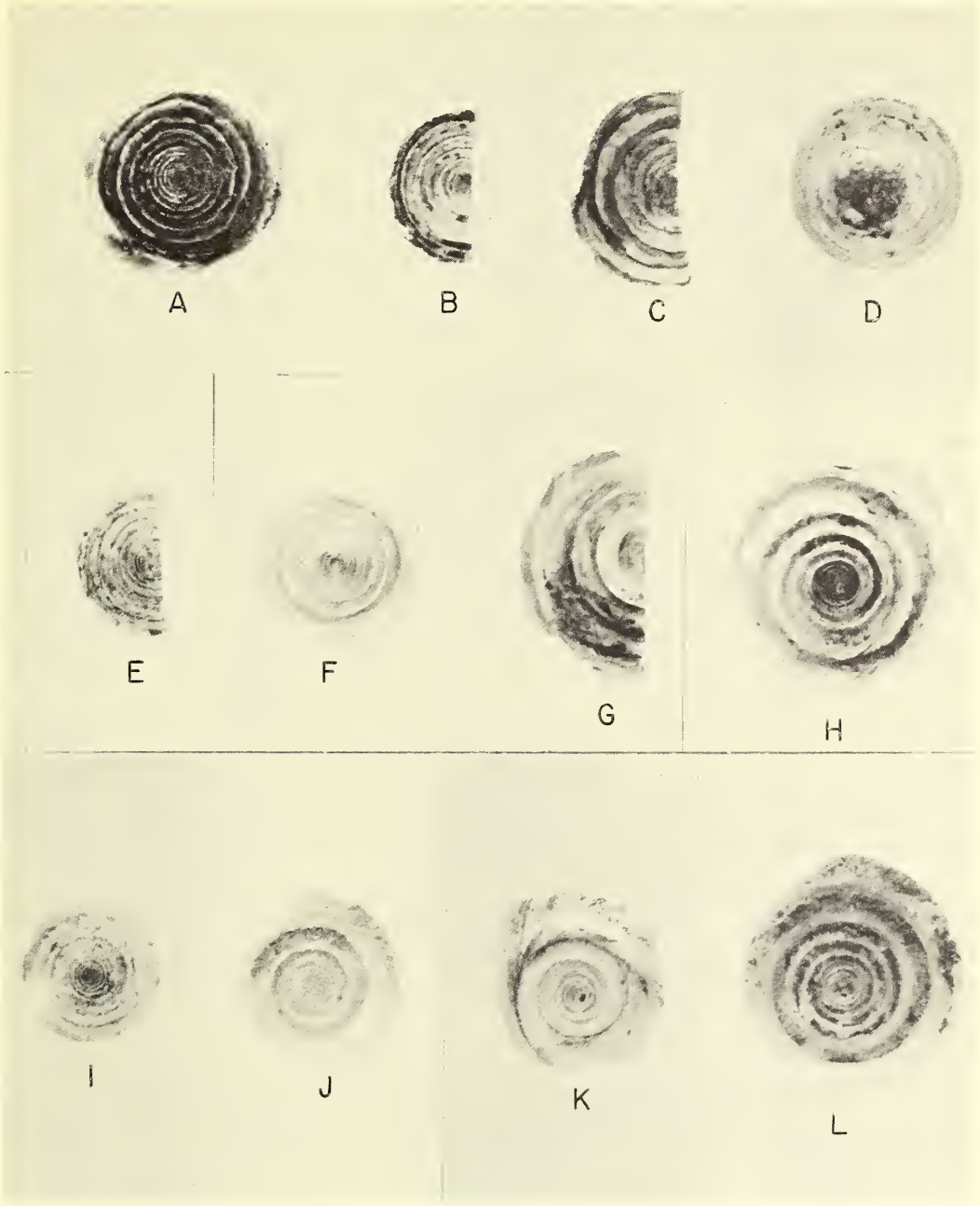
A-D. *Xenocyclus patulus* new species, holotype.
E-H. *Neocyclotus capscelius* new species, holotype.

Plate VI

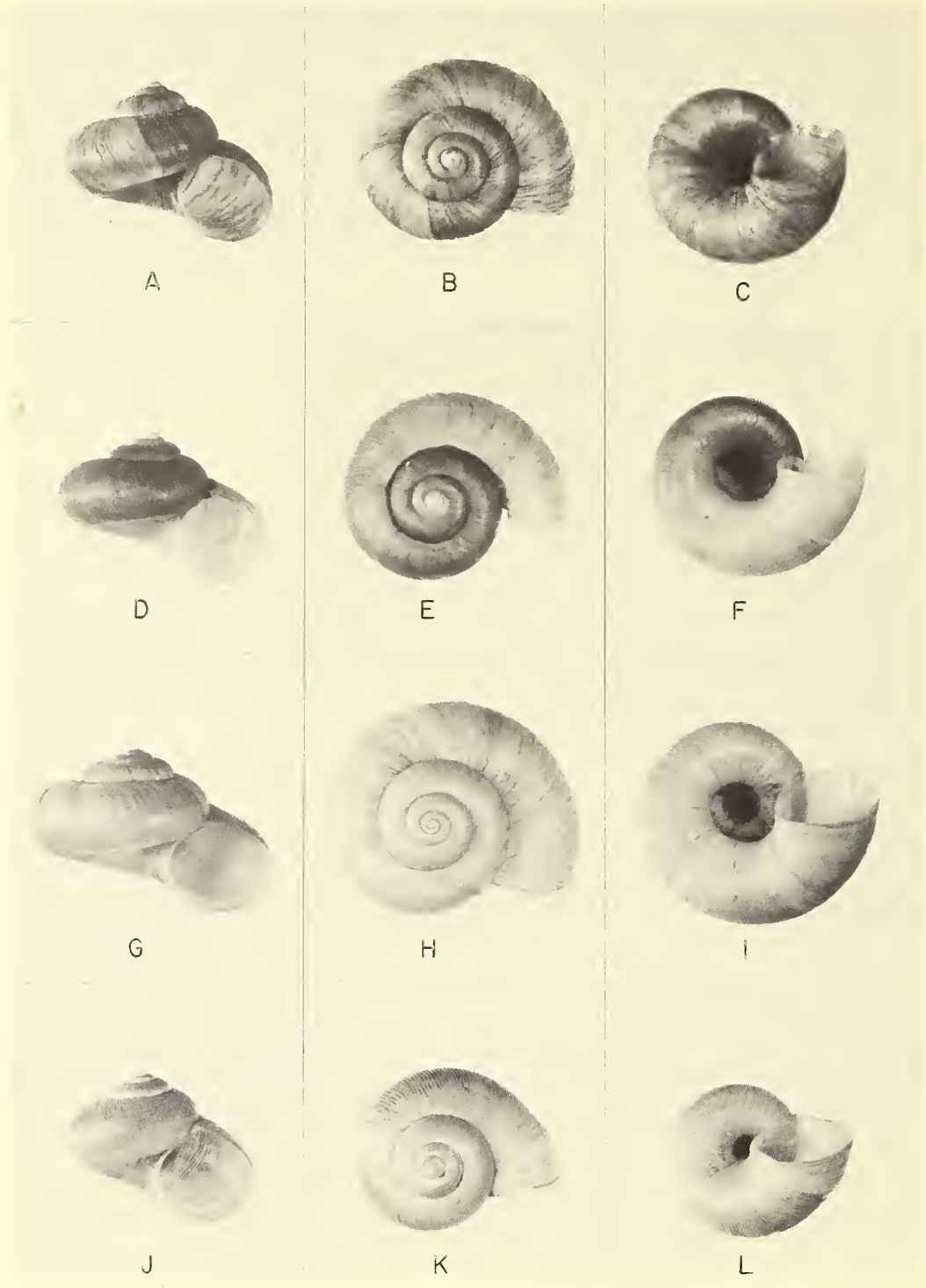
A-C. *Amphicyclotus texturatus spiralis* new subspecies, holotype.
D-F. *Amphicyclotus paulsonorum* new species, holotype.

Plate VII

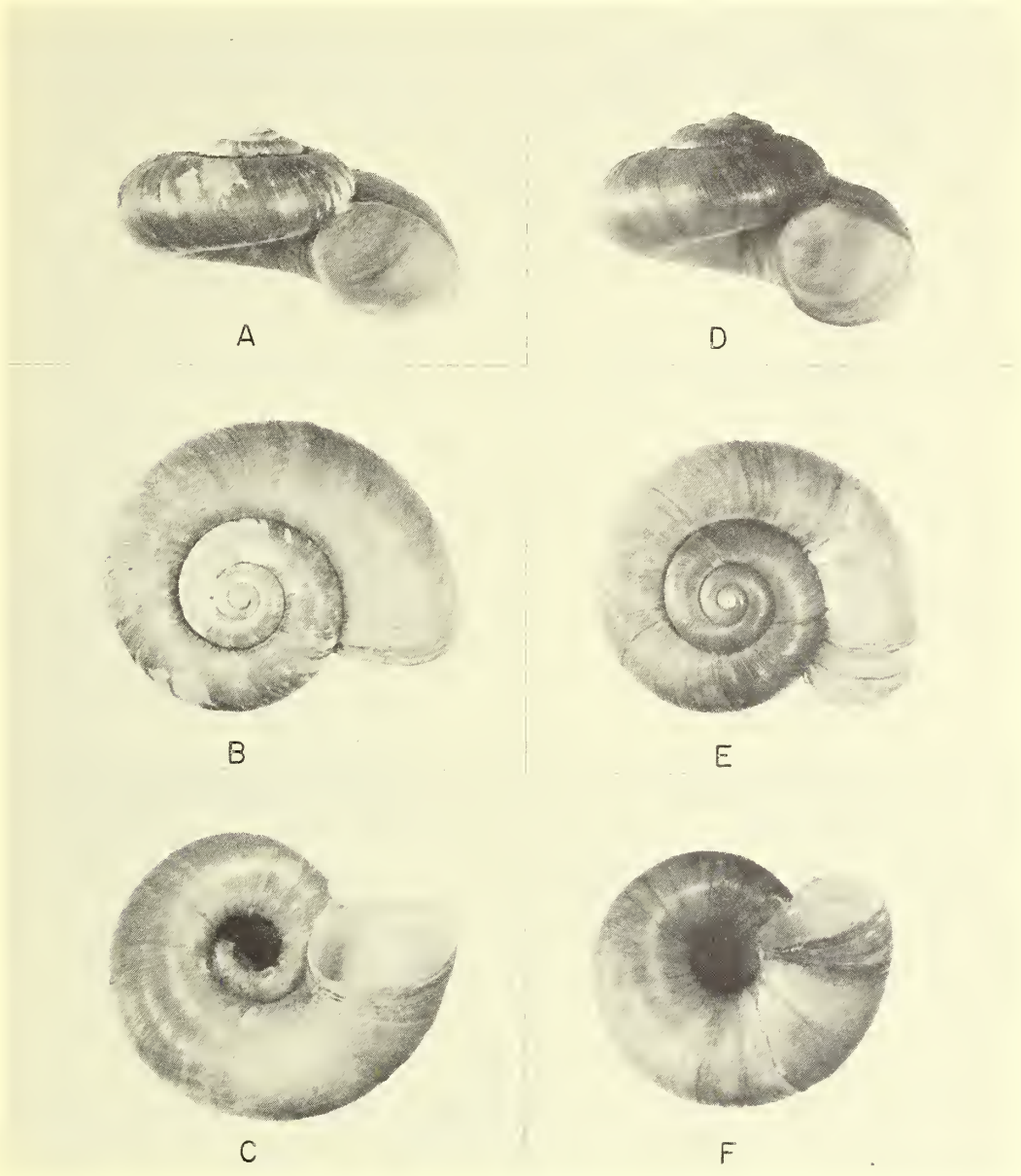
A-C. *Neocyclotus (Incidostoma) impressus* new species, holotype.
D-F. *Neocyclotus (Incidostoma) irregulare* (Pfeiffer), (UF 20150).
G. *Neocyclotus (Incidostoma) impressus* new species, paratype.



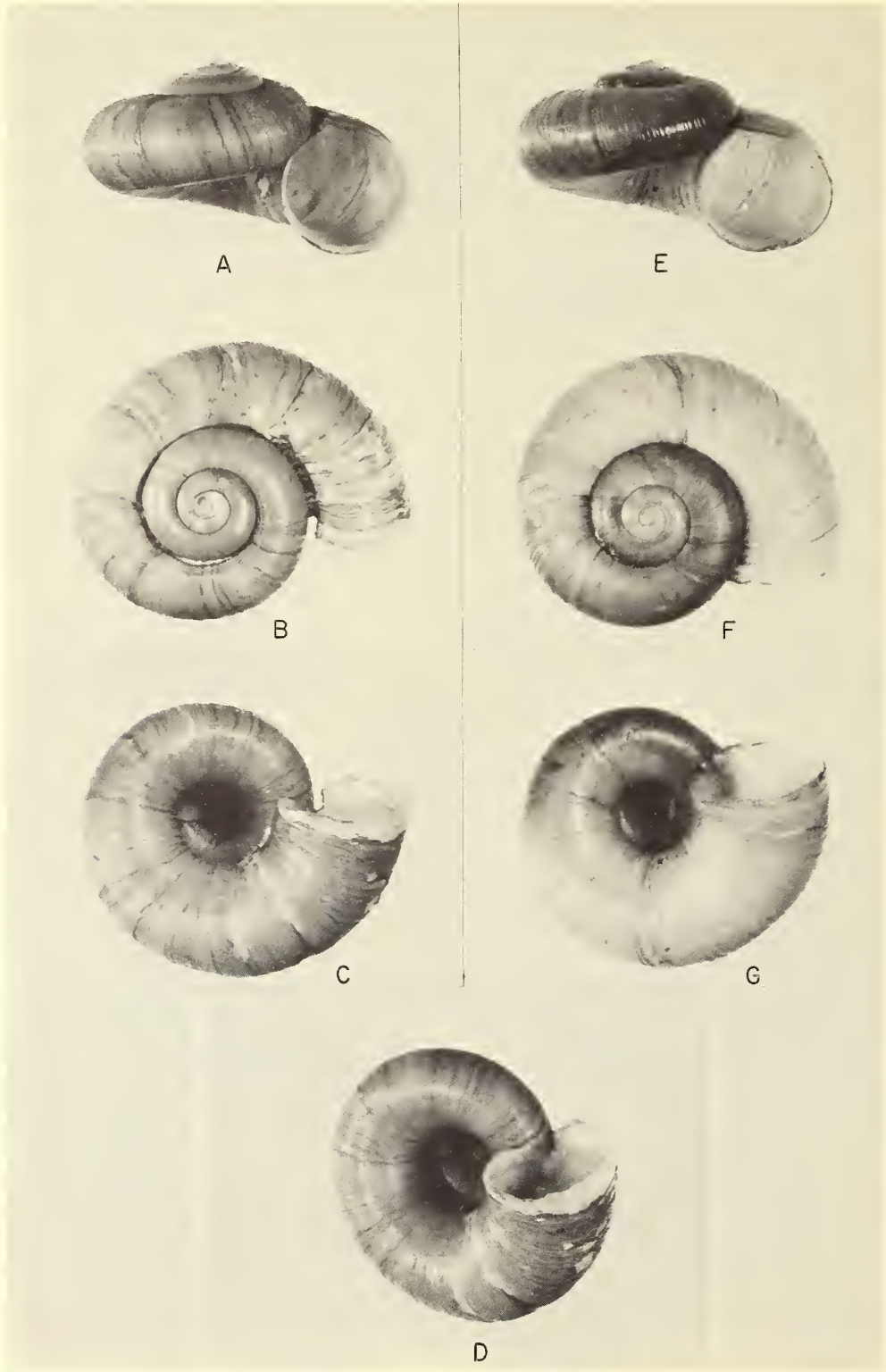
SOME MEXICAN AND CENTRAL AMERICAN
LAND SNAILS OF THE FAMILY CYCLOPHORIDAE



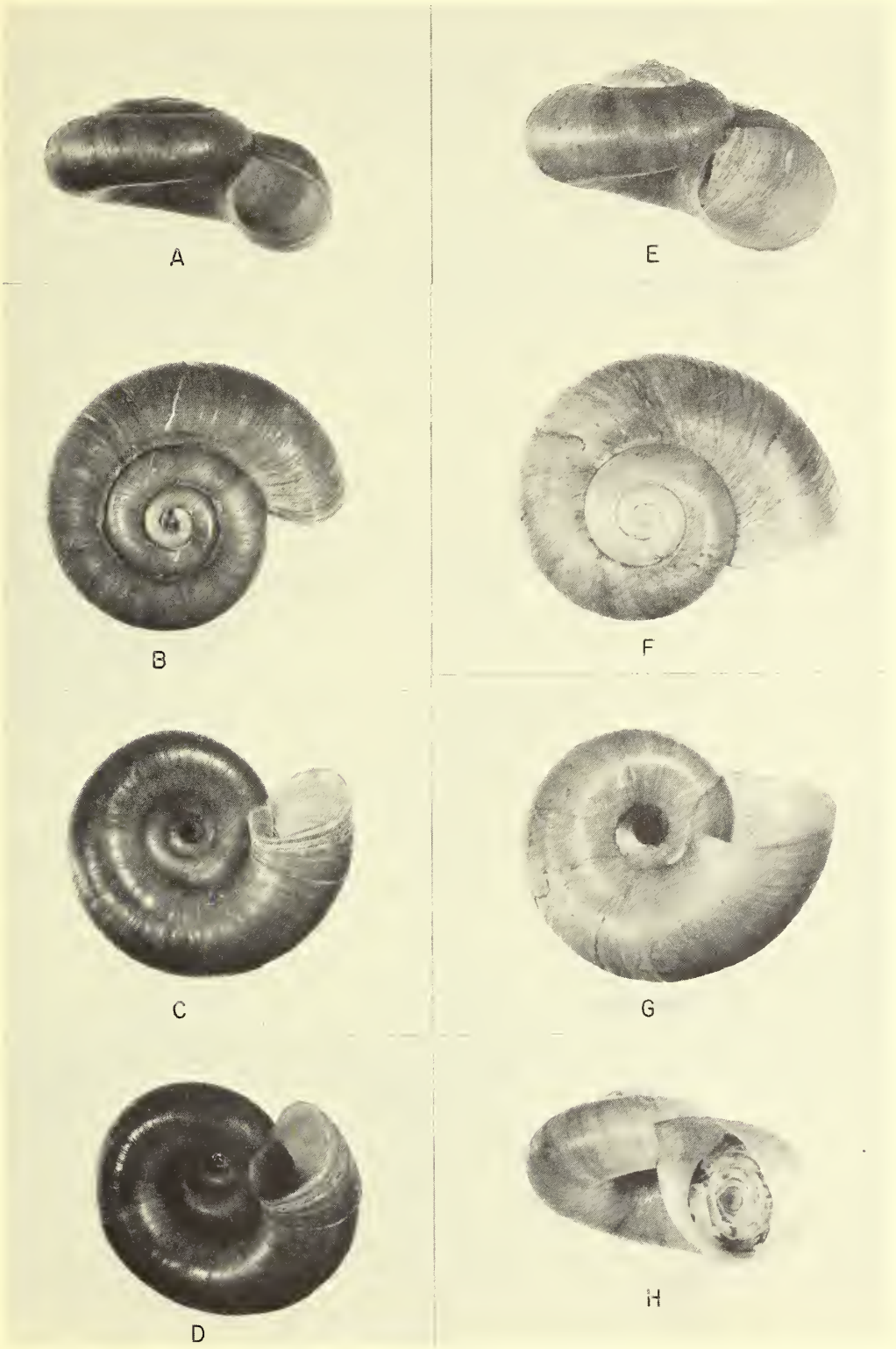
SOME MEXICAN AND CENTRAL AMERICAN
LAND SNAILS OF THE FAMILY CYCLOPHORIDAE



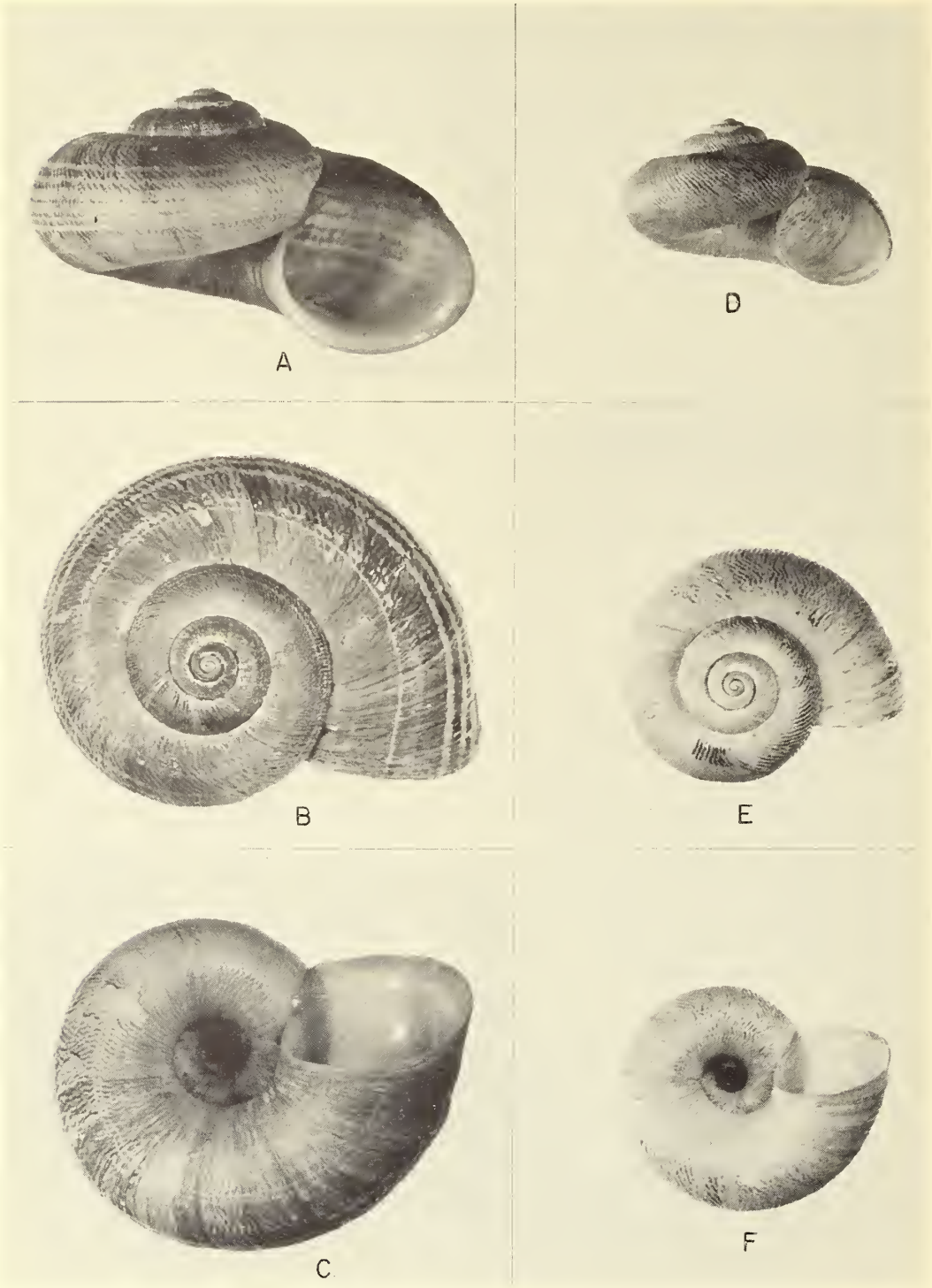
SOME MEXICAN AND CENTRAL AMERICAN
LAND SNAILS OF THE FAMILY CYCLOPHORIDAE



SOME MEXICAN AND CENTRAL AMERICAN
LAND SNAILS OF THE FAMILY CYCLOPHORIDAE



SOME MEXICAN AND CENTRAL AMERICAN
LAND SNAILS OF THE FAMILY CYCLOPHORIDAE



SOME MEXICAN AND CENTRAL AMERICAN
LAND SNAILS OF THE FAMILY CYCLOPHORIDAE

SOME MEXICAN AND CENTRAL AMERICAN
LAND SNAILS OF THE FAMILY CYCLOPHORIDAE

5

The Underwater Song of *Erignathus* (Bearded Seal)

CARLETON RAY,[1] WILLIAM A. WATKINS,[2]
AND JOHN J. BURNS[3]

(Plates I-III; Text-figure 1; Phonograph Disk)

Vocalization by mature males during breeding season. The call consists of a long oscillating frequency-modulated warble that may be more than a minute in duration, followed by a short unmodulated low-frequency moan. It typically starts at about 2000 cps with many frequency variations and ends as low as 200 cps. This call has been identified with the species by our own observations and those of others. Examination of seals heard calling and which were killed revealed them to be males in breeding condition. Thus, this "song" is apparently used solely by mature males in spring courtship season. It is suggested that its purpose is a proclamation of territory or of breeding condition or both.

INTRODUCTION

Erignathus barbatus (Erxleben, 1777), the bearded seal, produces a long combination of complicated underwater sounds during the spring courtship season. This we have termed the "song" because of its complex musical quality and apparent behavioral significance. The characteristic frequency-modulated warble and low moan, though produced entirely underwater, may occasionally be heard in air, radiating through the water surface or ice-cover or through the hull of the boat.

These musical underwater sounds have been identified with the bearded seal by the Eskimos who habitually hunt the species as a major source of food and skins (Burns, 1967). The association of singing sounds with the seals is reflected in the names used for these animals by the Alaskan Eskimos; when the seals are singing, the term that is used ("aveloouk" – Upik dialect; "ayuktuk" – Inupik dialect) is translated as "the one that sings" or "the singer." The reference is to the bearded seal (in-air known as "mukluk" or "oogruk," respectively).

The song of *Erignathus* was described by Peter Freuchen (1921-24: pp. 224-225) as a "shrill, siren-like note which is made in the water and becomes deeper and deeper till it ends in a long-drawn-out sigh." The sigh he described as a "strange, dull, deep-toned sound," remarking that some "sighs" were accompanied by bubbles which he thought indicated that the seal would shortly surface. The description fits the underwater sound very well and has been quoted by other more recent authors. Poulter (1966) has described the underwater signals of *Erignathus*, but the spectrographic analyses he presents are hard to compare with ours since no scale is indicated and a non-standard logarithmic frequency portrayal is used. It seems likely that these are sounds of *Erignathus*, but we do not find either the high (6 kcps) frequency starts or the consistently distinct pulses he describes.

Over the past 10 years two of us (C. R. and J. B.) have observed *Erignathus* in the Bering Sea. These observations have included a number of instances when the "singing" could definitely be attributed to a seal in the water. Usually only a part of the song was heard in-air as a seal was closely approached, but through a series

[1] Department of Pathobiology, School of Hygiene and Public Health, The Johns Hopkins University, Baltimore, Maryland 21205.

[2] Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543 (Contribution No. 2028 from WHOI).

[3] Division of Game, Alaska Department of Fish and Game, P.O. Box 862, Nome, Alaska 99762.

of such exposures a general impression of the song has been obtained. These impressions have been confirmed by underwater recordings made from shore, from pack ice, and from small boats on 7, 8, 9, 10, 14, 20, and 21 May 1966 near Gambell, St. Lawrence Island, Alaska (C. R.) and analyzed at Woods Hole Oceanographic Institution (W. W.). The dates of recording corresponded to the height of the courtship season. No other mammals were seen in the immediate vicinity during most of the listening periods, except for a few walrus, *Odobenus,* whose underwater sounds were noted to be similar to some of those reported from a captive (Schevill, Watkins, and Ray 1966).

The recordings were made with an LC-50 (Atlantic Research) hydrophone, a preamplifier (Watkins, 1963), and a Nagra III tape recorder. Analysis playback was by means of a Crown (800 series) recorder. The system was essentially flat from 50 to 10,000 cps. Spectrographic analyses were made on a Kay Electric Vibralyzer.

Acoustical Results

The song of *Erignathus* is both complicated and highly variable, yet by listening for an extended period an overall pattern for the song may be noted. The entire pattern occasionally is heard in one song; more often the song is fragmented with only parts of the song given and the variations predominating. At times a short rising trill may signal the repetition of a large part of the song, usually with additional variations. Our listening sample appears to have been large enough and from a sufficiently varied locale so as to offset limiting oceanographic factors, such as selective frequency attenuation and temperature/pressure effects. The fact that the song may be heard through the water-air interface indicates a relatively intense sound.

The song of *Erignathus* is a highly frequency-modulated call, much more so than that of any other marine animal we have herad. It may be continuous for more than a minute and is composed of short oscillations of the carrier-frequency (frequency-modulation) superimposed on longer-duration variations of the carrier-frequency. The song gives the aural impression of a long, siren-like oscillating warble. The song starts at 2000 to 3000 cps and ends at 200 to 300 cps; there is an overall downward sweep in frequency throughout the song, though there may be several short-term upward excursions. The song appears to end with a separate unmodulated low-frequency moan of two to three seconds duration and usually slightly decreasing frequency.

In our recordings, singing seals were numerous and never sufficiently isolated from their fellows to be certain of the attribution of the entire song to one individual. However, the pattern appeared generally to be the same. The variability noted in the detail of the pattern may be the result of individual preference.

Our representative song (Text-fig. 1) was as follows:

1) An introductory short warble which rose in frequency from 2500 to 3000 cps and lasted 2.5 seconds.

2) A second phrase 20 seconds in duration in which the carrier-frequency dropped from 3000 to 1000 cps.

3) A third phrase which lasted 3.5 seconds and rose to 2000 cps in carrier-frequency.

4) A repetition of phrase two with additional variations, 40 seconds in duration, which dropped to just below 1000 cps and was followed by a pause of 15 seconds.

5) An unmodulated moan which lasted 3 seconds and fell in frequency from 400 to 300 cps.

Detailed description of the song as heard from many individuals is as follows. The beginning phrase of the song (Pl. I) is a rising warble characterized by short bursts (100 to 250 msec. long) of frequency-modulation with oscillations of up to 1000-cps variation, separated by periods (100-150 msec.) of either less variation in frequency or unmodulated tone. This first phrase of the song may last 2.5 to 8 seconds.

The introductory phrase is followed by a long second phrase (Pl. II), an oscillating warble that may last a minute or more and that is composed of regular frequency oscillations produced at a relatively rapid rate (12-30 per second) superimposed on slower oscillations of the carrier frequency which vary at the rate of 3 per second to 1 per several seconds. The overall frequency drops during this phrase of the song and both the rapid frequency-modulation and the slower oscillation of the carrier-frequency occur progressively more slowly. Thus during the later portions of the second phrase, the song becomes more like a simple frequency-modulated warble in which the long carrier-frequency oscillations are of 5 to 10 seconds in duration. The sound may vary during frequency modulation by as much as 1000 cps, but the largest is usually about 500 cps.

A third phrase consisting of a short warble sometimes interrupts the second phrase, usually to be followed by a repetition of phrase two as another "verse" of varying length. This ascend-

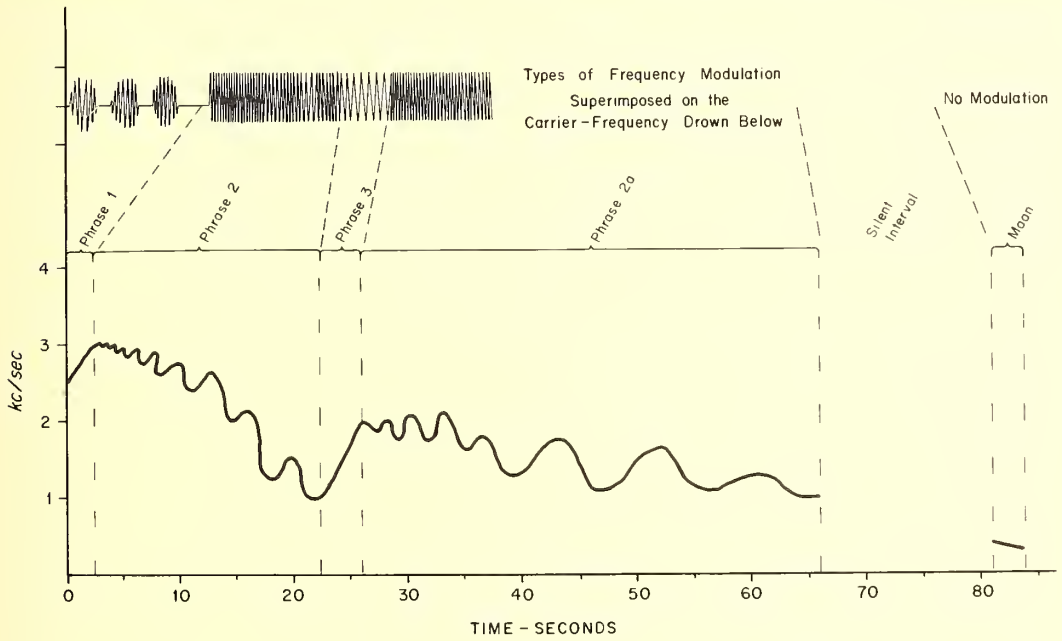
ing warble is relatively short (3 to 7 seconds) and has regular frequency-modulation as well as a steadily rising carrier-frequency (Pl. III). A typical insertion of the ascending trill into the song raises the carrier-frequency from about 1000 to 2000 cps allowing a repetition or a variation of the last portions of the song. The ascending warble is never used following a moan and is always inserted when the carrier-frequency of the song has dropped to 1000 cps or below.

The moan (lower portion, Pl. II) appears at the end of many of the *Erignathus* songs and so we include it as a part of the total song. Actually, there usually is a silence of up to 30 seconds (the interval is difficult to determine) between the last part of the slowly oscillating warble and the beginning of the moan. The moan is always lower in frequency than the earlier parts of the song. It is an unmodulated tone usually of descending frequency between 500 to 200 cps and of 2 to 3 seconds duration, contrasting sharply with the long frequency-modulated warble that precedes it. At close range, it is the moan that is associated with the appearance of bubbles and the subsequent surfacing of the seal.

Behavioral Observations

In spite of its superficial variability, the general pattern of the song of *Erignathus* is stereotyped and repetitive. It is complex and musical; it is seasonally produced and apparently sexually distinctive. It may also be territorial in function. In these respects the song of *Erignathus* fits the traditional usage of the term "song" as it is applied to the complex sound combinations of passerine birds.

In an effort to determine the role of the song a number of seals were collected (J. B.) It is the habit of *Erignathus* to swim in leads or openings in loose pack ice and individuals are not gregarious. Of 17 identified as singing and collected, all were males; of another 19 collected in the immediate vicinity of singing, 15 were males. All of these males proved to be sexually mature. Contrastingly, in July, though many seals of both sexes have been observed, none has been heard to sing. This strongly implies that the male *Erignathus* is proclaiming either its breeding territory in the pack ice or simply its availability or perhaps both. This is not in agreement with Freuchen's (1921-24) often quoted assertion that the song is used for communica-



Text-fig. 1. The lower portion of the drawing is a spectrographic portrayal of the characteristic (irregular sine-wave-like) variations in the carrier-frequency of an *Erignathus* song. Additional modulation is superimposed on these carrier-frequency variations and consists of relatively rapid frequency-modulation whose swing about the carrier-frequency may be as large as 1000 cps; this is portrayed in the upper portion of the drawing. During phrase one the frequency-modulation typically is in short bursts; phrase two has continuous but varying frequency modulation; phrase three has slower and more regular modulation; and the moan at the end is separated from the rest of the song by a silent interval and is unmodulated.

tion between mother and pup, nor with Poulter's (1966) evident belief that the song has a sonar function.

Our suggestions are reinforced by the observations of the Eskimos. Those that were interviewed agreed that the song is heard only from March through June and is associated with relatively short dives of about three minutes duration. They emphasized that bubbles always appear at the surface shortly after the moan is heard and that these bubbles are used as a convenient marker for the seal's appearance where it may be killed by the hunter.

The observation that in-air sound is used by phocid seals in territorial or courtship activities on land has been made for *Mirounga*, the elephant seal, by Bartholomew (1952). That sound is important in underwater courtship in its world of shore ice has also been suggested for *Leptonychotes*, the Weddell seal, by Ray (1967). Territory in the case of *Erignathus* would imply a lead or opening in the pack ice.

Summary and Conclusions

The underwater song of *Erignathus* usually consists of a long oscillating frequency-modulated warble that may be more than a minute in duration, followed by a short unmodulated low-frequency moan. The song typically starts at about 2000 cps with many frequency variations and ends as low as 200 cps. The song apparently is used only by mature males during the spring courtship season. It is suggested that its purpose is a proclamation of territory or of breeding condition or both.

Acknowledgments

We wish to thank Dr. F. H. Fay of the Arctic Health Research Laboratory, U. S. Public Health Service, College, Alaska, for aid in the identification of sounds. Winfred James and numerous eskimos of Gambell, Alaska, aided us in the field.

We also wish to thank W. E. Schevill and Dr. R. H. Backus, both of Woods Hole Oceanographic Institution, for many helpful criticisms during preparation of the manuscript. This work was sponsored by the following grants: the New York Zoological Society (C. Ray); the Arctic Institute of North America to The Johns Hopkins University under contractual agreements with the Office of Naval Research (C. Ray); the Office of Naval Research contract Nonr 4446 (W. A. Watkins); Federal Aid to Wildlife funds, Pittman-Robertson Project W-6-R and W-14-R (J. J. Burns).

Literature Cited

Bartholomew, G. A., Jr.

1952. Reproductive and social behavior of the northern elephant seal. Univ. Calif. Publ. Zool., 47:369-472.

Burns, J. J.

1967. The Pacific bearded seal. Alas. Dept. of Fish and Game. Juneau. 66pp.

Freuchen, P.

1921-4. Mammals. Part II, Rept. Fifth Thule Exped., 2(4 & 5):68-278.

Poulter, T. C.

1966. Systems of echolocation. *In* Les Systèmes Sonars Animaux, *Ed* R.-G. Busnel. Lab. Physiol. Acous., Jouy-en-Josas, France, 1:157-185.

Ray, Carleton

1967. Social behavior and acoustics of the Weddell seal. Antarctic Jour., 2(4):105-106.

Schevill, W. E., W. A. Watkins, and Carleton Ray

1966. Analyses of underwater *Odobenus* calls with remarks on the development and function of the Pharyngeal pouches. Zoologica, 51(3):103-105.

Watkins, W. A.

1963. Portable underwater recording system. Undersea Tech., 4(9):23-24.

EXPLANATION OF THE PLATES

PLATE I

The song of *Erignathus* begins with an introductory warble (phrase one) that alternates short bursts of frequency-modulation separated by periods of relatively unmodulated tone. The sounds below 2 kcps are from more distant seals. The analyzing filter bandwidth is 200 cps.

PLATE II

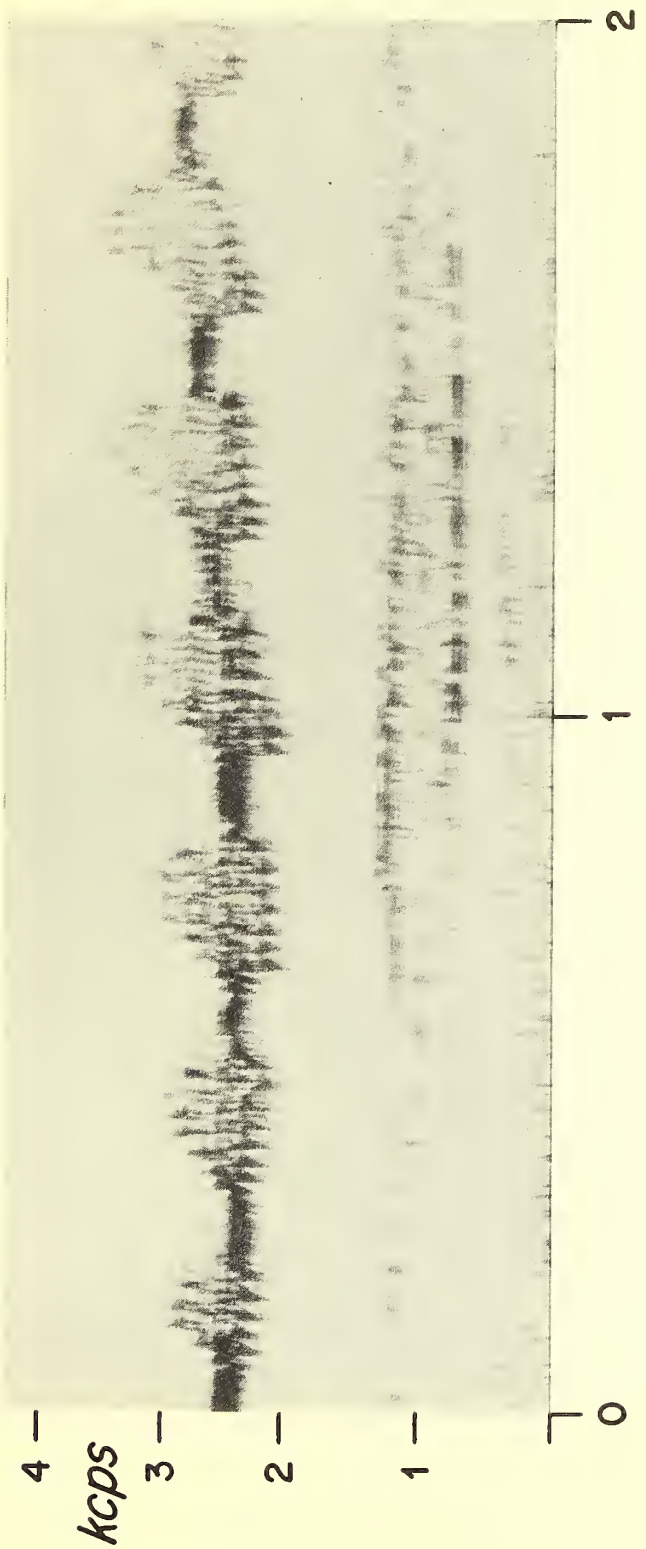
A later portion during the *Erignathus* song (phrase two) is portrayed in the upper part of the spectrogram and shows rapid frequency-modulation superimposed upon carrier-frequency oscillations of longer duration. The lower part illustrates a moan at the end of another seal's song. The effective filter bandwidth in this analysis is 120 cps.

PLATE III

Sometimes interrupting phrase two is a short rising warble (phrase three) in which short-term modulations are regular and there are no longer oscillations as in phrase two. The analyzing filter bandwidth is 400 cps.

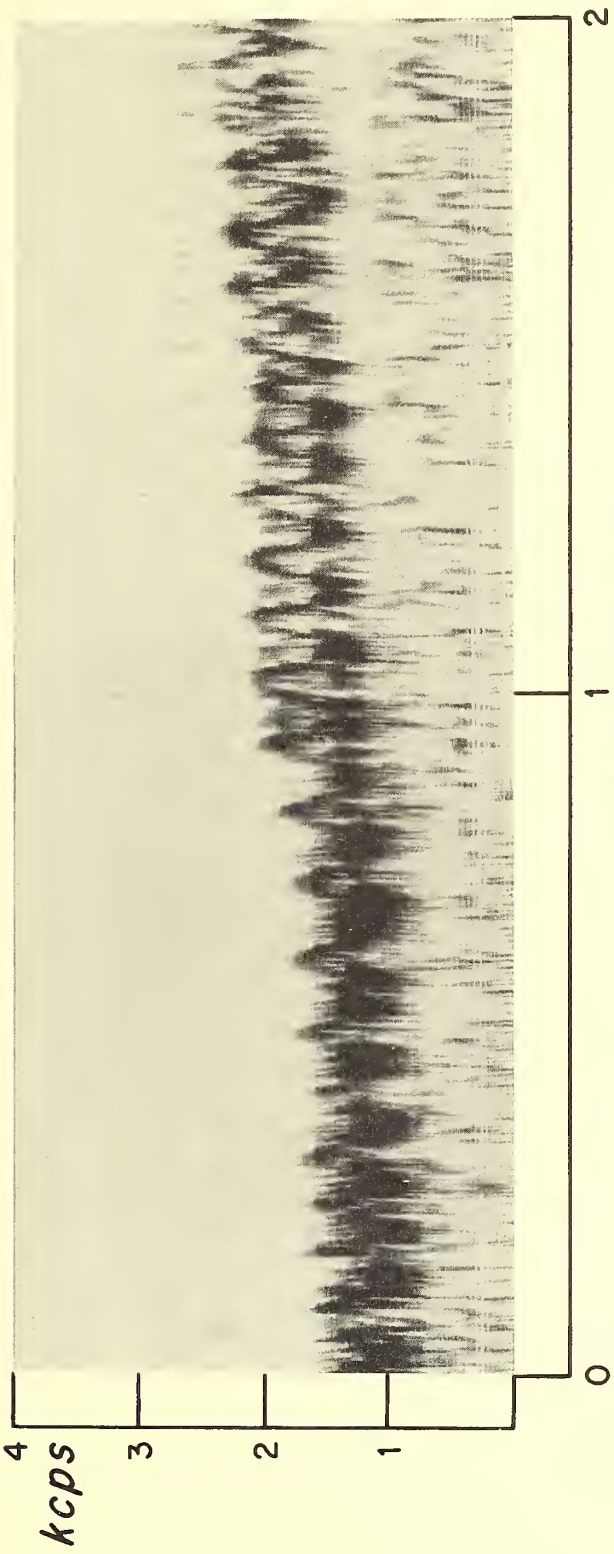
INSERTED

Phonograph disk of the underwater song of *Erignathus* (Bearded Seal).



THE UNDERWATER SONG OF ERIGNATHUS (BEARDED SEAL)

THE UNDERWATER SONG OF ERIGNATHUS (BEARDED SEAL)



THE UNDERWATER SONG OF ERIGNATHUS (BEARDED SEAL)

NEW YORK ZOOLOGICAL SOCIETY

The Zoological Park, Bronx, N. Y. 10460

OFFICERS

LAURANCE S. ROCKEFELLER, *President*
ROBERT G. GOELET, *Executive Vice-President, Chairman of the Executive Committee*
HENRY CLAY FRICK, II, *Vice-President*
JOHN PIERREPONT, *Treasurer*
HOWARD PHIPPS, JR., *Secretary*
EBEN W. PYNE, *Assistant Treasurer*

EDWARD R. RICCIUTI, *Editor & Curator, Publications & Public Relations*
JOAN VAN HAASTEREN, *Associate Editor*

EDITORIAL COMMITTEE

ROBERT G. GOELET, *Chairman*

WILLIAM G. CONWAY, HUGH B. HOUSE, PETER R. MARLER, DONALD R. GRIFFIN, F. WAYNE KING, ROSS F. NIGRELLI

WILLIAM G. CONWAY, *General Director*

ZOOLOGICAL PARK

William G. Conway . . . *Director & Curator, Ornithology*
Hugh B. House . . . . *Curator, Mammalogy*
Grace Davall . . *Assistant Curator, Mammals & Birds*
Walter Auffenberg . . . *Research Associate in Herpetology*
Joseph Bell . . *Associate Curator, Ornithology*
F. Wayne King . . . . *Curator, Herpetology*
William Bridges . *Curator of Publications Emeritus*
John M. Budinger . . . *Consultant, Pathology*
Ben Sheffy . . . . . *Consultant, Nutrition*
James G. Doherty . *Assistant Curator, Mammalogy*
Donald F. Bruning . . . . . *Ornithologist*
Joseph A. Davis, Jr. . . . . *Scientific Assistant to the Director*

AQUARIUM

Ross F. Nigrelli . . . . . *Director*
Christopher W. Coates . . . *Director Emeritus*
Nixon Griffis . . . . *Administrative Assistant*
Robert A. Morris . . . . . *Curator*
U. Erich Friese . . . . . *Assistant Curator*
Louis Mowbray . *Research Associate in Field Biology*

OSBORN LABORATORIES OF MARINE SCIENCES

Ross F. Nigrelli . . . *Director and Pathologist*
Martin F. Stempien, Jr. . . . *Assistant to the Director & Bio-Organic Chemist*
George D. Ruggieri, S.J. . . . *Coordinator of Research & Experimental Embryologist*
William Antopol . . . *Research Associate in Comparative Pathology*
C. M. Breder, Jr. . . . *Research Associate in Ichthyology*
Jack T. Cecil . . . . . *Virologist*
Harry A. Charipper . . *Research Associate in Histology*
Kenneth Gold . . . . . *Marine Ecologist*
Myron Jacobs . . . . . *Neuroanatomist*
Klaus Kallman . . . . . *Fish Geneticist*
Vincent R. Liguori . . . . . *Microbiologist*
John J. A. McLaughlin . . *Research Associate in Planktonology*
Martin P. Schreibman . . *Research Associate in Fish Endocrinology*
Jay Hyman . . . . . *Research Associate in Comparative Pathology*

INSTITUTE FOR RESEACH IN ANIMAL BEHAVIOR

[Jointly operated by the Society and The Rockefeller University, and including the Society's William Beebe Tropical Research Station, Trinidad, West Indies]

Donald R. Griffin . . . . *Director & Senior Research Zoologist*
Peter R. Marler . . . *Senior Research Zoologist*
Jocelyn Crane . . . *Senior Research Ethologist*
Roger S. Payne . . . . . *Research Zoologist*
Richard L. Penney . . . . *Research Zoologist*
Fernando Nottebohm . . . *Research Zoologist*
George Schaller . . . . . *Research Zoologist*
Thomas T. Struhsaker . . . *Research Zoologist*
C. Alan Lill . . . . . *Research Associate*
O. Marcus Buchanan . . . *Resident Director, William Beebe Tropical Research Station*
Paul Mundinger . . . . . *Research Associate*